



Defining the stock structures of key commercial tunas in the Pacific Ocean I: Current knowledge and main uncertainties



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ABSTRACT

Tunas are the focus of significant fisheries in the Pacific Ocean, where landings of four species – skipjack tuna (*Katsuwonus pelamis*), yellowfin tuna (*Thunnus albacares*), bigeye tuna (*Thunnus obesus*) and albacore tuna (*Thunnus alalunga*) – constitute approximately 70 % of the global tuna catch. Stock assessments for skipjack, yellowfin and bigeye tunas in the Pacific Ocean currently assume eastern and western stocks. For albacore tuna, separate North Pacific Ocean and South Pacific Ocean stocks are currently assumed. In each case, these geographic definitions reflect the historical development of fisheries management across the Pacific rather than biological considerations. There is widespread agreement that uncertainties surrounding the stock structures of these four tuna species could have important impacts on the population dynamics models used to assess their status and inform management options. Knowledge of stock structure is also essential for improved modelling of the effects of climate change on tuna distribution and abundance and associated implications for fisheries. This paper reviews current knowledge and understanding of the stock structures of skipjack, yellowfin, bigeye and South Pacific albacore tunas in the Pacific Ocean, by exploring available literature relating to their biology, movement and spatial dynamics. As a guide for future research in this area, we identify the main uncertainties in defining the stock structure of these four tunas in the Pacific, including i) spawning dynamics; ii) the degree of spawning area fidelity and localised residency; iii) the provenance of individuals in, and proportional contributions of self-replenishing populations to, fishery catches within the Pacific Ocean; iv) linkages with adjacent 'stocks'; v) the effects of climate change on stock structure and proportional contributions of self-replenishing populations to fisheries; and vi) the implications of improved knowledge of tuna stock structure for stock assessment and climate change model assumptions and fisheries management. We also briefly propose some approaches that future studies could use to address these uncertainties.

1. Introduction

Tunas (Family Scombridae, Tribe Thunnini) are ecologically important top-order predators in pelagic ocean ecosystems (Sund et al.,

1981; Young et al., 2010). They occur across tropical to sub-polar habitats and support extensive fisheries worldwide (FAO, 2018; Reglero et al., 2014). In the Pacific Ocean, tunas support major industrial fisheries and a variety of small-scale domestic and subsistence fisheries.

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The principal target species are skipjack tuna (*Katsuwonus pelamis*), yellowfin tuna (*Thunnus albacares*), bigeye tuna (*Thunnus obesus*), and albacore tuna (*Thunnus alalunga*). Combined, these four species comprise over 90 % of industrial tuna catches from the Pacific Ocean and approximately 70 % of global commercial tuna catches (SPC-OPF, 2018a).

The majority of catches for each of these four tuna species from the Pacific Ocean comes from the tropical and sub-tropical waters of the Western and Central Pacific Ocean (WCPO) (Fig. 1), with an estimated 2.5 million metric tonnes (mt) harvested commercially in 2017 (SPC-OPF, 2018a). Substantial harvests of tuna are also made in the Eastern Pacific Ocean (EPO), with an estimated 637,397 mt of skipjack, yellowfin and bigeye tunas caught in 2017 (IATTC, 2018).

Management of tuna fisheries in the Pacific Ocean, whose distributions straddle exclusive economic zones (EEZs) and the high seas, is coordinated primarily through two international conventions: the Convention on the Conservation and Management of Highly Migratory Fish Stocks in the Western and Central Pacific Ocean¹; and the Antigua Convention² (which revised the Convention for the Establishment of an Inter-American Tropical Tuna Commission). These conventions are operationalised by two independent tuna Regional Fisheries Management Organisations (tRFMOs): the Western and Central Pacific Fisheries Commission (WCPFC) in the WCPO, and the Inter-American Tropical Tuna Commission (IATTC) in the EPO.

Current assessments for skipjack, yellowfin and bigeye tunas assume single stocks of each species in the WCPO and the EPO, whereas separate North Pacific Ocean and South Pacific Ocean stocks are assumed for albacore tuna. In each case, these geographic definitions reflect the historical development of fisheries management across the Pacific rather than biological features of the species that might be considered in population assessments. Further, regional structures within stock assessments, when present, typically represent the spatial distribution of fishing gears with differing selectivities, tag mixing assumptions, and management regimes (McKechnie et al., 2014; Tremblay-Boyer et al., 2017, 2018; Vincent et al., 2019). There is growing evidence, however, that the spatial structure and population dynamics of these four target tunas may be more complex than currently assumed. Complexities in stock structure, if present at scales different to those currently assumed in the population dynamics models used to assess stock status, may have important implications for stock assessments and fisheries management arrangements. For example, undertaking a stock assessment based on a single closed stock within a defined area when there are multiple individual stocks within the area, or assessing only a portion of a larger stock, is likely to produce misleading results (Begg et al., 1999). Failure to recognise stock structure can lead to under-fishing of stocks with high productivity if overly conservative population parameters are assumed, or over-fishing of less productive stocks should less conservative population parameters be assumed (Begg et al., 1999; Tuck and Possingham, 2000). Where stocks may be undergoing rebuilding from past over-harvesting, differential restoration between unidentified stock components can lead to an inability to anticipate future recruitment to those stocks (Begg et al., 1999; Kell et al., 2009). Inappropriate assumptions of stock structure may also have implications for model-based investigations of the effects of climate change on the distribution and abundance of the four tuna species (e.g., Lehodey et al., 2017; Senina et al., 2018). Models to date have assumed that single, self-replenishing populations exist for each of the four tuna species across the Pacific basin. Defining stock structure for the four tuna species is thus considered to be a key research priority for fisheries management (WPRFMC, 2014; Kolody and Hoyle, 2015; Kumar and Kocour, 2015;

Evans et al., 2016; Pecoraro et al., 2017) and essential for planning effective adaptation of the region's tuna fisheries to climate change (SPC, 2019).

With the aim of updating current understanding of the movement and stock structure of skipjack, yellowfin, bigeye and South Pacific albacore tunas in the Pacific, an international workshop was held in Nouméa, New Caledonia, in October 2018. The objectives of the workshop were to: 1) review the current understanding of movement and stock structure of these four tuna species in the Pacific Ocean, and define and discuss the main related knowledge gaps and uncertainties; and 2) outline sampling considerations and approaches aimed at reducing these gaps and uncertainties. The workshop focused on these four species due to their importance to fisheries throughout the Pacific, their overlap in habitats (particularly as adults), their collective management under the two tRFMOs in the Pacific, and their importance to Pacific Island countries and territories (PICTs). Here, we provide a synthesis of the current knowledge and understanding relating to the biology, movement and spatial dynamics of these four species used to guide the workshop discussions. With the perspective that self-replenishing populations should be the basic unit of fisheries management, we examine the relevant biology and spatial considerations in current stock assessment approaches for each tuna species, and review published research on their movement, connectivity and stock structure in the region. Recognising that genetic approaches provide the only direct evidence of gene flow, this latter discussion is split into genetic and non-genetic studies, noting and comparing results of any multi-disciplinary studies where relevant. We then outline the main knowledge gaps and uncertainties to defining the stock structure of the four species in the Pacific Ocean, and identify some approaches that future studies could adopt to address these gaps.

2. Current understanding of the stock structures of skipjack, yellowfin, bigeye and South Pacific albacore tunas in the Pacific Ocean

2.1. Skipjack tuna

2.1.1. Relevant biology and spatial considerations in stock assessment approaches

Skipjack tuna are broadly distributed across the Pacific Ocean, inhabiting tropical to temperate waters from the equator to around 35° of latitude in the WCPO, extending to around 40°N and 43°S with the seasonal extensions of warm poleward flowing currents (Blackburn and Serventy, 1981; Kiyofuji et al., 2019). In the EPO, their distribution narrows to approximately 15° of latitude from the equator east of about 145°W, extending to around 30°N and 25°S seasonally offshore from the Americas (Sund et al., 1981; Matsumoto et al., 1984). The bulk of skipjack tuna biomass, however, occurs within 10° of latitude from the equator (Fig. 1). Tagging and fishery catch data suggest that the distribution of skipjack tuna may vary with the El Niño-Southern Oscillation (ENSO), with an eastwards shift in core distribution to the central Pacific Ocean (CPO) under El Niño conditions (Lehodey et al., 1997).

Based on observations of gonad state of mature individuals and the distribution of larvae, spawning in skipjack tuna is considered to occur in both the WCPO and EPO where sea surface temperatures (SSTs) generally exceed 24 °C, with the greatest proportion of spawning occurring in waters between 26 °C and 29 °C (Nishikawa et al., 1985; Schaefer, 2001a; Servidad-Bacordo et al., 2012; Ashida and Horie, 2015; Schaefer and Fuller, 2019). This is considered to result in year-round spawning in tropical waters with spawning occurring seasonally elsewhere across the species' distribution (Schaefer and Orange, 1956; Orange, 1961; Schaefer and Fuller, 2019; Ohashi et al., 2019). Off Japan, for example, gonad weights of skipjack tuna are relatively higher in May and June than in other months (Yabe, 1954), with fish observed with spent ovaries in July and August. Larval densities of skipjack tuna are higher in the WCPO than in the EPO, suggesting the main spawning

¹ <https://www.wcpfc.int/doc/convention-conservation-and-management-highly-migratory-fish-stocks-western-and-central-pacific>.

² https://www.iatcc.org/PDFFiles/IATTC-Instruments/_English/IATTC_Antigua_Convention%20Jun%202003.pdf.

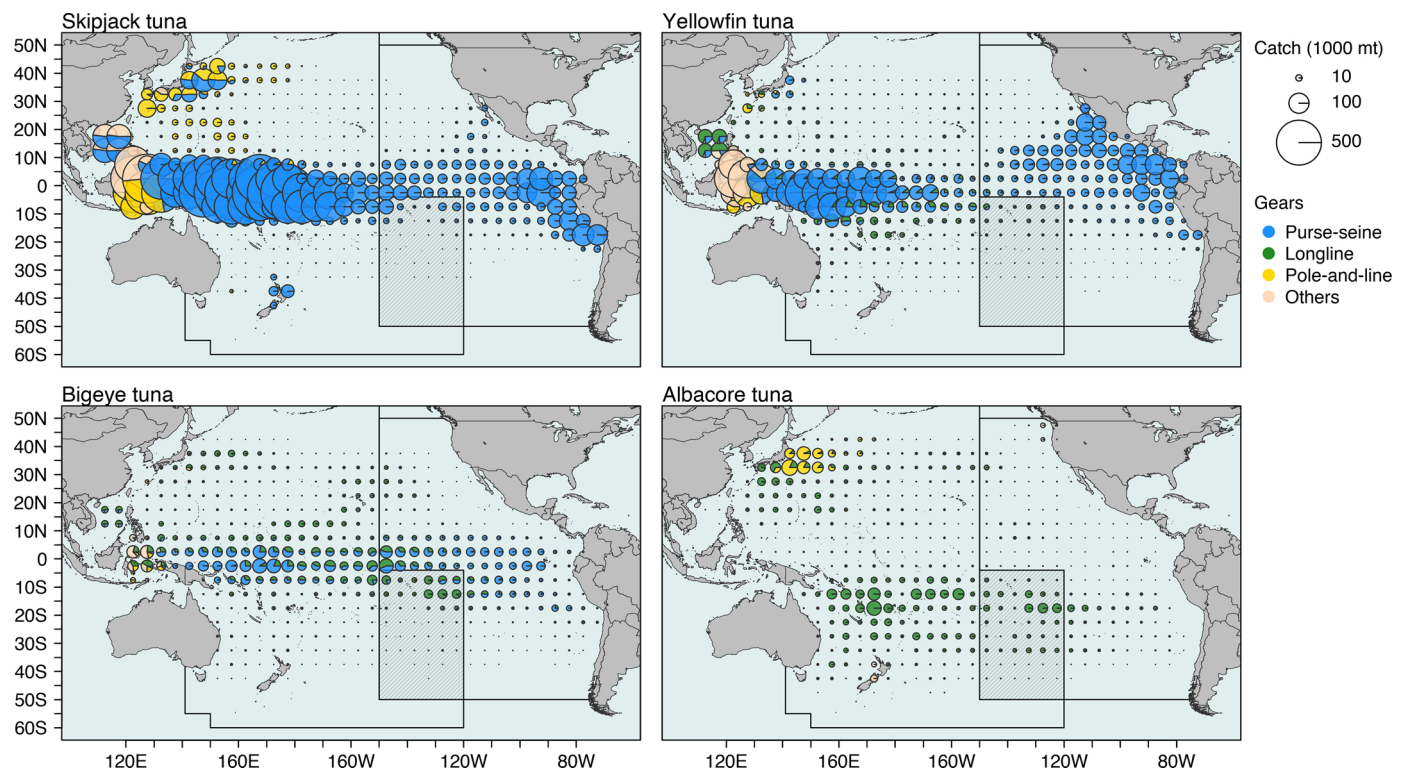


Fig. 1. Distribution and magnitude of total catches for skipjack, yellowfin, bigeye and albacore tunas in the Pacific Ocean between 2009–2018 by 5° square and fishing gear: purse-seine (blue), longline (green), pole-and-line (yellow) and others (pink). The shaded area represents the overlap in management area between the Western and Central Pacific Fisheries Commission (WCPFC; west) and Inter-American Tropical Tuna Commission (IATTC; east) Convention Areas. Note that pies are positioned at the centre of each 5° square and only those catches > 1 mt are shown. Source: Pacific Community (SPC), supplemented by IATTC Public Domain Data (available at: <https://www.iattc.org/PublicDomainData/IATTC-Catch-by-species1.htm>). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

areas are in the WCPO (Ueyanagi, 1969; Matsumoto et al., 1984; Nishikawa et al., 1985), although it should be noted that there has been comparatively less sampling effort in the EPO. Patchy distribution of skipjack tuna larvae in the Phoenix Islands Protected Area has been proposed to occur as a result of spatial variability in the distribution of spawning individuals (Hernández et al., 2019).

Several studies have explored the degree to which schools of skipjack tuna maintain their temporal integrity. Sharp (1978) found evidence of genetic similarity between individuals in ‘core’ schools, concluding that there was a high probability that some members of the schools were siblings. Based on parasite assemblages, Lester et al. (1985) estimated that schools maintain their integrity for several weeks, but not for life. From conventional tagging data, Bayliff (1988a) estimated that schools of skipjack tuna maintain integrity for weeks to months, while Hilborn (1991) concluded that schools in the WCPO ‘do not appear to remain composed of the same individuals for more than a few weeks’. Based on ultrasonic tracking of individuals associated with drifting fish aggregating devices (FADs) across temporal scales of hours to a few days, Schaefer and Fuller (2013) concluded that tagged skipjack tuna were not a cohesive unit, and that the associated schools did not exhibit a high degree of permanence in structure or size.

In the WCPO, the stock assessment area for skipjack tuna extends from 20°S to 50°N (Vincent et al., 2019). The 2019 assessment was split into eight regions (Fig. 2), based on the nature of the operating fleets (purse-seine fleets operating in equatorial waters, artisanal fisheries taking a large proportion of the catch in the westernmost region, and pole-and-line fleets active throughout much of the area but particularly in the northern and westernmost regions), seasonal movement dynamics and differences in size composition for the pole-and-line fleets in the northern regions, and tag mixing assumptions around release sites (Vincent et al., 2019).

In the EPO, the last formal stock assessment was conducted in 2005 and was considered uncertain due to unreliable indices of abundance (Maunder and Harley, 2005). Indicators of stock status are now used to monitor skipjack tuna in the EPO (Maunder and Deriso, 2007; Maunder, 2019), which implicitly assume a single stock. Spatially structured assessment models have been explored (e.g., Maunder, 2012), but to date there has been insufficient information for catch-per-unit-effort (CPUE) and length-composition data to provide reliable estimates of stock size for most candidate sub-populations of skipjack tuna in the EPO.

2.1.2. Genetic studies

Studies applying genetic approaches to skipjack tuna in the Pacific Ocean have identified varying levels of population structure. Based on blood groups, two phenotypes were identified from fish caught around Hawaii (Cushing, 1956). Variability in blood groups was also identified from fish caught around Hawaii and French Polynesia (Marquesas, Tuamotu and Society Islands), suggesting isolated populations (Sprague and Holloway, 1962). Using blood groups and isozymes, Fujino (1970) proposed the occurrence of two skipjack tuna groups across the Pacific Ocean: a ‘western Pacific’ population, including fish sampled from the east coast of Japan, Marcus Islands, Bonin-Marianas and Palau, and a ‘central east Pacific’ population, including samples from Baja California, Ecuador, French Polynesia (Society Islands), Line Islands and Hawaii. From genetic, conventional tagging and size distribution data, Fujino (1996) identified three sub-populations of skipjack tuna within this central east Pacific population: the central west Pacific, the central northeast Pacific, and the central southeast Pacific. Fujino (1996) further identified that fish from each group occurred in Hawaiian waters at different times of the year, and proposed that archipelagos and ocean currents played a significant role in their observed structuring, with, for example, the Izu-Bonin-Mariana-Caroline archipelagos delineating the

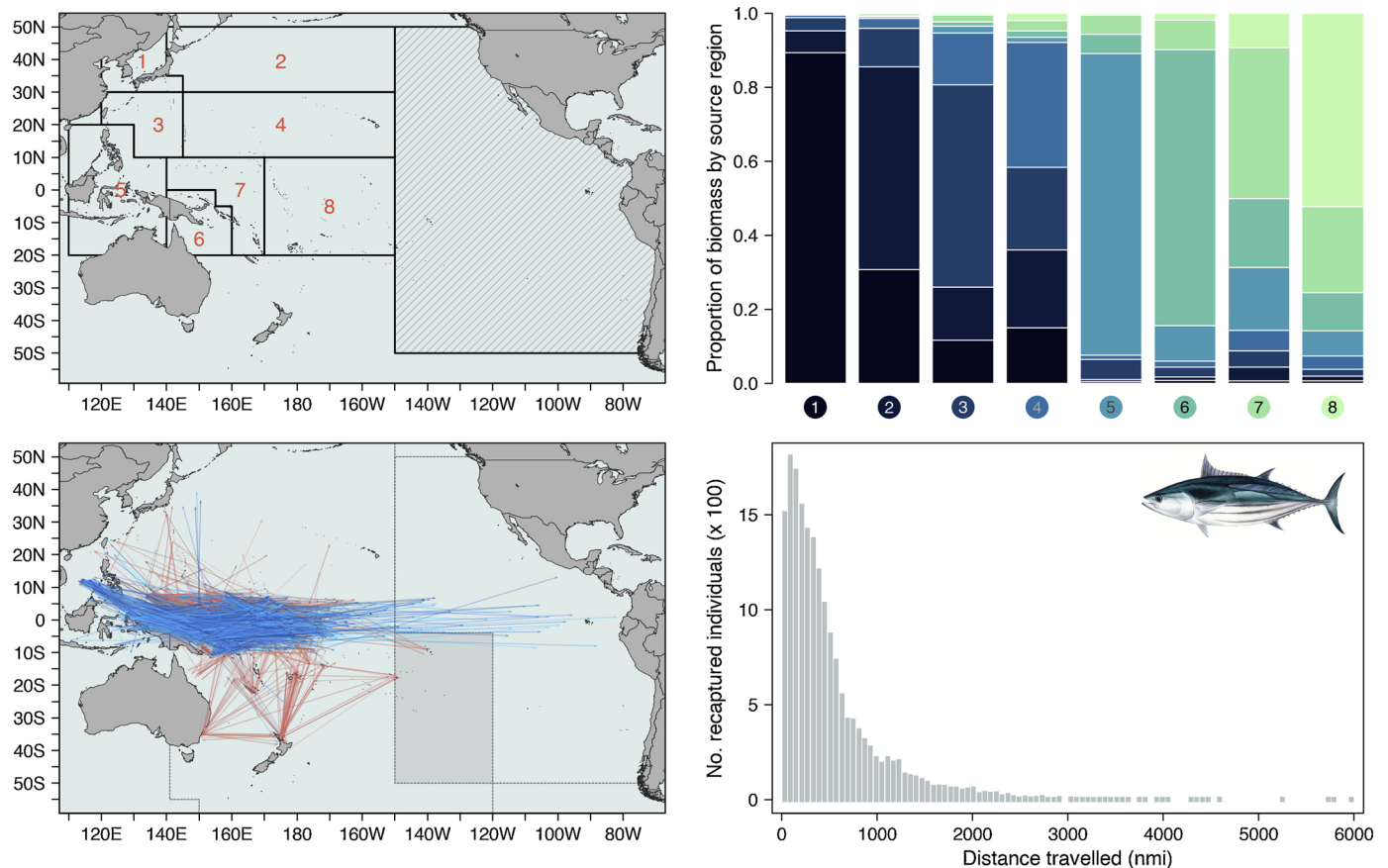


Fig. 2. Top left: The geographic area and regional structure used in the recent stock assessments of skipjack tuna in the Western and Central Pacific Ocean (WCPO; numbered areas) and Eastern Pacific Ocean (EPO; line shaded area) by Vincent et al. (2019) and Maunder (2019), respectively; bottom left: movements of skipjack tuna tagged during the Regional Tuna Tagging Programme (RTTP; red arrows) and the Pacific Tuna Tagging Programme (PTTP; blue arrows) recaptured > 1000 nmi from their release point; top right: proportional distribution of total biomass by weight in each WCPO assessment region apportioned by the source regions; bottom right: distribution of observed tag displacements for skipjack tuna at liberty for ≥ 3 months from RTTP and PTTP data. All tagging data shown are based on SPC holdings. Skipjack tuna image: Les Hata, © SPC. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

westward limit of the range of the central west Pacific population. Fujino (1996) concluded that the observed geographical genetic heterogeneities could not be attained without the combination of isolation by distance and homing for spawning, although noted there was no direct evidence for the latter.

Heterogeneity in allozyme markers has been observed in skipjack tuna caught around Japan and Hawaii, whereas no differences were found between fish from Hawaii and Palau (Fujino and Kang, 1968). Variability in allozyme markers has also been used to propose at least five ‘subpopulations’ of skipjack tuna with overlapping geographical boundaries in the Pacific Ocean (New Zealand, north-eastern Pacific, south-eastern Pacific, north-western Pacific, and Papua New Guinea / Solomon Islands) (Sharp, 1978). Observing spatial clines in enzyme allele frequencies, Richardson (1983) proposed an isolation-by-distance model for skipjack tuna in the Pacific, with the average radius of a genetic neighbourhood in the order of ~1080 nautical miles (nmi).

DNA isolation, mtDNA D-loop region amplification and nucleotide sequence analyses failed to detect any genetic differentiation between skipjack tuna samples from Solomon Islands in the western Pacific Ocean (WPO) and those from the EPO (Ely et al., 2005). Furthermore, no differences were found in these markers between skipjack tuna sampled in the Pacific and Atlantic Oceans, a result which Ely et al. (2005) suggested was likely due to the large effective population sizes of skipjack tuna in each basin.

More recently, Grewe et al. (2019) used next generation sequencing (NGS) approaches and single nucleotide polymorphism (SNP) makers to

investigate population structuring of skipjack tuna in the Indian and Pacific Oceans. Based on a preliminary analysis the authors report significant differentiation between skipjack tuna sampled from the EPO and the Indo-Pacific (Maldives, Bismarck and Coral Seas), but not among their Indo-Pacific sampling locations.

2.1.3. Non-genetic studies

Skipjack tuna has been the primary focus of a number of dedicated, large-scale, conventional tagging programmes conducted in both the WCPO and EPO. In the WCPO, these studies date back to the 1970s, commencing with the Skipjack Survey and Assessment Programme (SSAP; 1977–1981). Large numbers of skipjack tuna have since been tagged through the Regional Tuna Tagging Programme (RTTP; 1990–1996), which operated in waters between the Philippines and the Phoenix Islands of Kiribati, including off the east coast of Australia, and the Pacific Tuna Tagging Programme (PTTP; 2006–present), operating in waters 10°N–10°S; 120°E–130°W (Hampton and Gunn, 1998; Leroy et al., 2015). Combined, these three programmes have tagged over 469,000 skipjack tuna to date, with over 65,000 recoveries reported by June 2018, including almost 47,000 recoveries of skipjack tuna tagged in the PTTP alone (Leroy et al., 2015; SPC-OFP, 2018b). Within the WCPO, these programmes have been complemented by a number of national-level tagging activities (Leroy et al., 2015). In the EPO, tagging operations have been conducted by the IATTC since the 1950s. Around 130,000 skipjack tuna had been tagged by 2015, with 1426 recoveries deemed suitable for analyses of movement by Fonteneau and Hallier (2015).

Results from these programmes demonstrate that the movement dynamics of skipjack tuna are both spatially and temporally complex. In the WCPO, tagged skipjack tuna have been recaptured well in excess of 1000 nmi from original tagging locations (Fig. 2), with displacements increasing with fish size (SPC-OFP, 2015). The majority of recaptures of skipjack tuna tagged in the WCPO, however, suggest that long-distance movements are uncommon, with 95 % of skipjack tuna tagged in the SSAP, for example, being recaptured within 1000 nmi of their original release point (Fig. 2) (Hilborn and Sibert, 1998). Sibert and Hampton (2003) estimated skipjack tuna tagged during the SSAP and RTTP to have a median lifetime displacement ranging from 420 to 470 nmi. Modelling suggests comparatively low rates of movement for tagged fish in the region surrounding Solomon Islands (Kleiber and Hampton, 1994; SPC-OFP, 2017). Notwithstanding issues associated with time-at-liberty, the distribution of tag releases and the distribution and variability of fishing effort (Leroy et al., 2015), observations from these programmes suggest the potential for some degree of regional fidelity of skipjack tuna.

Seasonality of movements of skipjack tuna in the Pacific Ocean has also been proposed. Using a combination of conventional tagging, genetic and size distribution data, Fujino (1996) hypothesised that fish from the WCPO follow two routes to waters off Japan with the extension of the Kuroshio Current in late spring: one from Hawaii through the Midway Islands, and a second moving northward from the Mariana-Bonin-Izu archipelagos. Both groups are then considered to return to tropical waters with the Kuroshio Current Extension in late autumn (Fujino, 1996). From archival tagging data, Kiyofuji et al. (2019) observed strong seasonality in movement of skipjack tuna tagged in the sub-tropical waters south of Japan between 17 °N and 28 °N and the Kuroshio Extension Area north of 28 °N, with northward movement of fish from subtropical areas (20°–30 °N) commencing in spring. In contrast, individuals tagged in waters surrounding the Nansei Islands, south-west of mainland Japan, were considered to display greater residency to that area, at least over the duration these fish were at liberty (12–402 days). In the southwestern Pacific Ocean, tag returns suggest skipjack tuna move south along the Australian east coast during the austral summer, reaching as far as Tasmania before returning to tropical waters in late autumn and winter (Blackburn and Serventy, 1981).

Tagging data from the EPO suggest a similar mix of seasonally cyclical movement, limited large-scale displacements, and regional fidelity, as well as extensive offshore-onshore movements (Fink and Bayliff, 1970; Bayliff, 1984, 1988b). Based on conventional tagging data, Fink and Bayliff (1970) concluded that there appear to be two main 'groups' of skipjack tuna in the EPO: a northern group, occurring around Baja California, the Gulf of California, and the Revillagigedo Islands off the coast of Mexico, and a southern group, occurring from Central America (~Panama) south to northern Chile, with some exchange between groups. The origins of the two groups are largely uncertain, with some authors (e.g., Rothschild, 1965) hypothesising that they both originate from spawning in the central equatorial Pacific Ocean east of 130 °W. However, significant spawning is known to occur in waters of the EPO where SST is 24 °C or higher (Schaefer, 2001a), and fish in spawning condition have since been reported off the coasts of Panama and Ecuador (Schaefer, 2001a; Schaefer and Fuller, 2019), suggesting that at least some proportion of fish in both groups may result from local spawning.

Movements appear to differ between the two groups of skipjack tuna in the EPO. In general, fish in the northern group undertake a northern and then southern movement between 20 °N and 30 °N, coincident with the seasonal movement of the 20 °C surface water isotherm (Fink and Bayliff, 1970). The movements of the southern group appear to be more complex than those of the northern group (Fink and Bayliff, 1970). Young fish that appear in the Panama Bight appear to move either northward or southward along the coast, before returning to equatorial waters as adults to spawn (Schaefer, 2001a). Movements of skipjack tuna tagged in the EPO into the WCPO have also been

documented, although the proportion of fish observed to undertake such displacements is low, with only 27 fish of the almost 130,000 tagged in the EPO having been recaptured in the WCPO; 21 of which have been recaptured around Hawaii (Bayliff, 1988b).

Differences in morphometrics and growth rates of skipjack tuna have been reported at varying spatial scales (Hennemuth, 1959; Sibert et al., 1983; Bayliff, 1988b), suggesting some spatial structuring of individuals in the region. Ianelli (1993) observed temporal differences in recruitment of skipjack tuna in EPO and in the waters around Hawaii, indicating they had originated from different spawning events. Within the EPO, significant spatial variation in estimates of maturity at length have been reported for skipjack tuna in waters north of 15 °N, between 15 °N and 5 °S, and south of 5 °S (Schaefer and Fuller, 2019). Differences in growth rates of larval and juvenile skipjack tuna collected from two of the main ecological provinces comprising the Pacific Ocean – the Western Pacific Warm Pool and the North Pacific Tropical Gyre (Longhurst, 2006) – have also been observed, suggesting that these fish had grown under differing environmental conditions (Ashida et al., 2018). Lester et al. (1985) found no evidence that would support the presence of more than one parasitological stock of skipjack tuna in the Pacific.

Few studies have been published on the otolith chemistry of skipjack tuna. An investigation into the ontogenetic patterns in otolith Sr:Ca ratios of skipjack tuna (32.2–58.2 cm fork length (FL)) collected from the tropical western Pacific (Marshall Islands and Palau) and off the coast of Japan reported results consistent with a mix of individual movement behaviours (Arai et al., 2005). Sr:Ca ratios suggested that most skipjack tuna sampled from the Marshall Islands were resident in tropical waters. Elemental ratios in one individual suggested that this fish had moved into a temperate region after hatching, before returning to the Marshall Islands prior to capture (Arai et al., 2005). Sr:Ca ratios in the otoliths of most fish from Japan suggested they had originated in the tropics and moved to temperate waters (Arai et al., 2005), consistent with conclusions from tagging data (Aoki et al., 2017).

Based on tagging, size, catch and CPUE data, the most recent stock assessment for skipjack tuna in the WCPO estimated that biomass in the northernmost assessment regions (Regions 1–3) largely results from self-recruitment with exchange between these regions (Fig. 2) (Vincent et al., 2019). Biomass in Region 4 (encompassing Hawaii and the northern Marshall Islands) was estimated to result predominantly from these three regions, as well as from self-recruitment. Biomass in Region 5 (Indonesia and the Philippines) and Region 6 (northern Australia, Papua New Guinea and north-western Solomon Islands) was estimated to result largely from self-recruitment, whereas biomass in Region 7 and Region 8 was estimated to result predominantly from recruitment from regions encompassing the equator (Fig. 2) (Vincent et al., 2019). Overall, the model estimated little exchange of biomass between regions north and south of 10 °N. However, the lack of north-south mixing estimated by the model could be due in part to low reporting rates observed by vessels from particular countries whose vessels are active in the North Pacific Ocean (Peatman et al., 2019).

An ecosystem model (the Spatial Ecosystem and Population Dynamics Model (SEAPODYM; Lehodey et al., 2008)) estimates mean optimal spawning temperatures for skipjack tuna to be between 28.5–29 °C (Senina et al., 2016). These results generally match observations that skipjack tuna spawn nearly continuously in the Western Pacific Warm Pool (e.g., Nishikawa et al., 1985), where such temperatures are most consistent. Occasional seasonality of high and low larval densities in the Bismarck Sea are predicted during May–November, and December–February, respectively (Senina et al., 2016). Seasonally favourable areas for spawning of skipjack tuna are predicted in the EPO as occurring during April–June, partially matching observations of spawning in that region by Schaefer and Orange (1956) (although contrasting with more recent observations of Schaefer and Fuller (2019)), the central equatorial Pacific in May–August, and the north-west East China Sea in August–October (Senina et al., 2016).

A larval dispersal model (the Individual-based Kinesis, Advection and Movement of Ocean Animals model (Ikamoana; [Scutt Phillips et al., 2018](#))) estimated quarterly transfer rates of skipjack tuna between the Solomon and Bismarck Seas to the oceanic Western Pacific Warm Pool of greater than 10 % in both directions, with a transfer of up to 42 % from the former to the latter during a La Niña event ([Scutt Phillips et al., 2018](#)). Simulated transfer of fish between the Western Pacific Warm Pool and central equatorial Pacific under non-El Niño conditions was also high. Exchange between the EPO and the WCPO appeared to be relatively low, dominated by a quarterly influx of between 5%–15% of EPO biomass moving into the central equatorial region ([Scutt Phillips et al., 2018](#)).

2.1.4. Synthesis of available information on skipjack tuna stock structure

Based on observations to date, there is some evidence for structuring of skipjack tuna at broad spatial scales within the Pacific Ocean. Genetic studies (e.g., [Sharp, 1978](#); [Fujino, 1996](#); [Grewe et al., 2019](#)) have demonstrated varying degrees of structure between the EPO and WCPO, although results between methodologies, and the markers used, have not always been consistent. Finer-scale genetic structuring within the EPO and WCPO is largely unclear. This is in part because genetic studies conducted on skipjack tuna in the Pacific Ocean to date have generally been constrained by design and logistical issues, including a lack of structured sampling, sample sizes and limitations associated with the choice of markers investigated (see Section 3). A comprehensive assessment using NGS approaches across the Pacific Ocean has yet to be conducted. Tagging data (e.g., [Hilborn and Sibert, 1998](#); [Bayliff, 1984, 1988b](#)) suggest movements of skipjack tuna in the Pacific Ocean are both spatially and temporally complex, but generally support genetic results that indicate restricted movement of skipjack tuna between the EPO and the WCPO. In equatorial waters, where the bulk of tagging has been conducted, the majority of tagged individuals appear to exhibit regional fidelity, suggesting the potential for complex structuring within this area, although movement with seasonal expansions of habitat have also been observed. Identifying the self-replenishing populations from which individuals undertaking such movements originate will be key to resolving stock boundaries and dynamics ([Moore et al., this issue](#)). However, several caveats exist around the use of tagging data to resolve stock structure of skipjack tuna, relating to the types of tags used, tag return rates and distributions and uncertainties associated with population representativeness (see Section 3). In parallel, information from body morphometrics ([Hennemuth, 1959](#)), growth patterns (e.g., [Sibert et al., 1983](#); [Ashida et al., 2018](#)) and reproductive biology ([Schaefer and Fuller, 2019](#)) also indicate potential spatial structuring and residency of Pacific skipjack tuna at varying spatial scales, however the actual number of stocks present, their boundaries, and the manner by which they are structured, remains unresolved.

The regional fidelity indicated by tagging and biological data suggests that Pacific Ocean skipjack tuna may exhibit finer-scale and more complex structuring than that currently assumed in assessment models. However, fishery data indicate a continuous distribution of skipjack tuna in tropical waters of the EPO and WCPO ([IATTC, 2018](#); [Williams and Reid, 2019](#)), while the observation of at least some tagged individuals undertaking large-scale movement ([Fig. 2](#)) indicates the potential for a degree of broad-scale gene flow among regions. As such, the occurrence of multiple, genetically distinct and non-overlapping populations of skipjack tuna in each of the EPO and WCPO is unlikely, at least without some additional structuring mechanism, such as fish returning to specific areas for spawning (a form of spawning area fidelity; see Section 3). Unlike those tuna species for which such behaviour is proposed (e.g., Atlantic bluefin tuna, *Thunnus thynnus*; [Block et al., 2005](#)), there is little evidence for specific, isolated spawning areas for skipjack tuna, or for the cyclical movement patterns typically associated with fish returning to specific spawning areas.

Potentially more plausible is that the limited movements displayed

by the majority of individual skipjack tuna in equatorial waters may result in an isolation by distance structure, whereby increasing genetic differentiation is correlated with increasing distance. The observations of [Richardson \(1983\)](#), who proposed an isolation by distance model for Pacific Ocean skipjack tuna based on spatial clines in enzyme allele frequencies, and conclusions of [Fujino \(1996\)](#), are consistent with this hypothesis. Alternatively, the regional fidelity exhibited by most fish, coupled with occasional broad-scale movement and gene flow of individuals and/or larval dispersal among regions, may result in a metapopulation structure, or a series of population units wherein individual units exhibit dynamics that are largely determined by local demography, but are also influenced to a non-trivial degree by exchange with other units ([Kritzer and Sale, 2004](#); [Sale et al., 2006](#), and references therein). The observed differences in demographic parameters such as growth rates, maturity profiles and spawning dynamics are consistent with such a structure. Further sampling is required to test these various hypotheses.

2.2. Yellowfin tuna

2.2.1. Relevant biology and spatial considerations in stock assessment approaches

Yellowfin tuna are broadly distributed across the Pacific Ocean, inhabiting tropical to temperate waters from approximately 30°N to 30°S, extending to 40° in both hemispheres seasonally ([Sund et al., 1981](#)). The locations and timing of spawning of yellowfin tuna across the Pacific have been inferred from patterns of larval distribution and histological examinations of gonad condition. These data suggest that spawning occurs year-round in tropical waters, and seasonally at higher latitudes when surface water temperatures are generally above 24 °C ([Nishikawa et al., 1985](#); [Schaefer, 1998](#); [Itano, 2000](#)), although spawning has been recorded in surface water temperatures of as low as 21.5 °C ([Schaefer, 1998](#)). In the EPO, the greatest proportion of spawning occurs in waters between 26 °C and 30 °C ([Schaefer, 1998](#)). Yellowfin tuna are considered to be serial spawners, capable of repeated spawning at near daily intervals during each spawning event ([McPherson, 1991](#); [Schaefer, 1996](#); [Itano, 2000](#)). Key areas in which individuals have been observed spawning include the Banda Sea in Indonesia, the north-western Coral Sea, the eastern and southern Philippines, northeast of Solomon Islands, and around Fiji ([McPherson, 1988, 1991](#); [Gunn et al., 2002](#); [Servidad-Bacordo et al., 2012](#)). On the basis of gonad maturity and larval distribution data, [Suzuki et al. \(1978\)](#) identified three 'relatively discrete areas of intensive spawning activity along the equatorial zone', corresponding to the WPO (with spawning peaking in the third and fourth quarters of the year), CPO (with spawning peaking in the second and third quarters) and EPO (with spawning peaking in the first and second quarters).

The most recent assessment for yellowfin tuna in the WCPO ([Tremblay-Boyer et al., 2017](#)) incorporated a 9-region structure across the area 50°N–40°S ([Fig. 3](#)). Spatial structuring of the assessment was informed by the nature of the operating fleets (longline vessels targeting larger individuals and operating primarily in temperate waters; purse-seine vessels catching smaller individuals and operating almost exclusively in equatorial waters), and tag mixing assumptions, with additional spatial areas introduced along the longitudinal axes to increase east-to-west resolution ([McKechnie et al., 2014](#)). Assessment models used in the EPO do not currently incorporate any spatial component explicitly but adopt a 'fleets-as-areas' approach, which assumes several fisheries that are defined by partitioning the data in space and act on the stock with differing catchabilities and selectivities ([Mintev-Verá et al., 2019](#)).

2.2.2. Genetic studies

Early genetic investigations into the structure of yellowfin tuna in the Pacific Ocean included those of [Barrett and Tsuyuki \(1967\)](#), who did not identify any heterogeneity among yellowfin tuna sampled in the

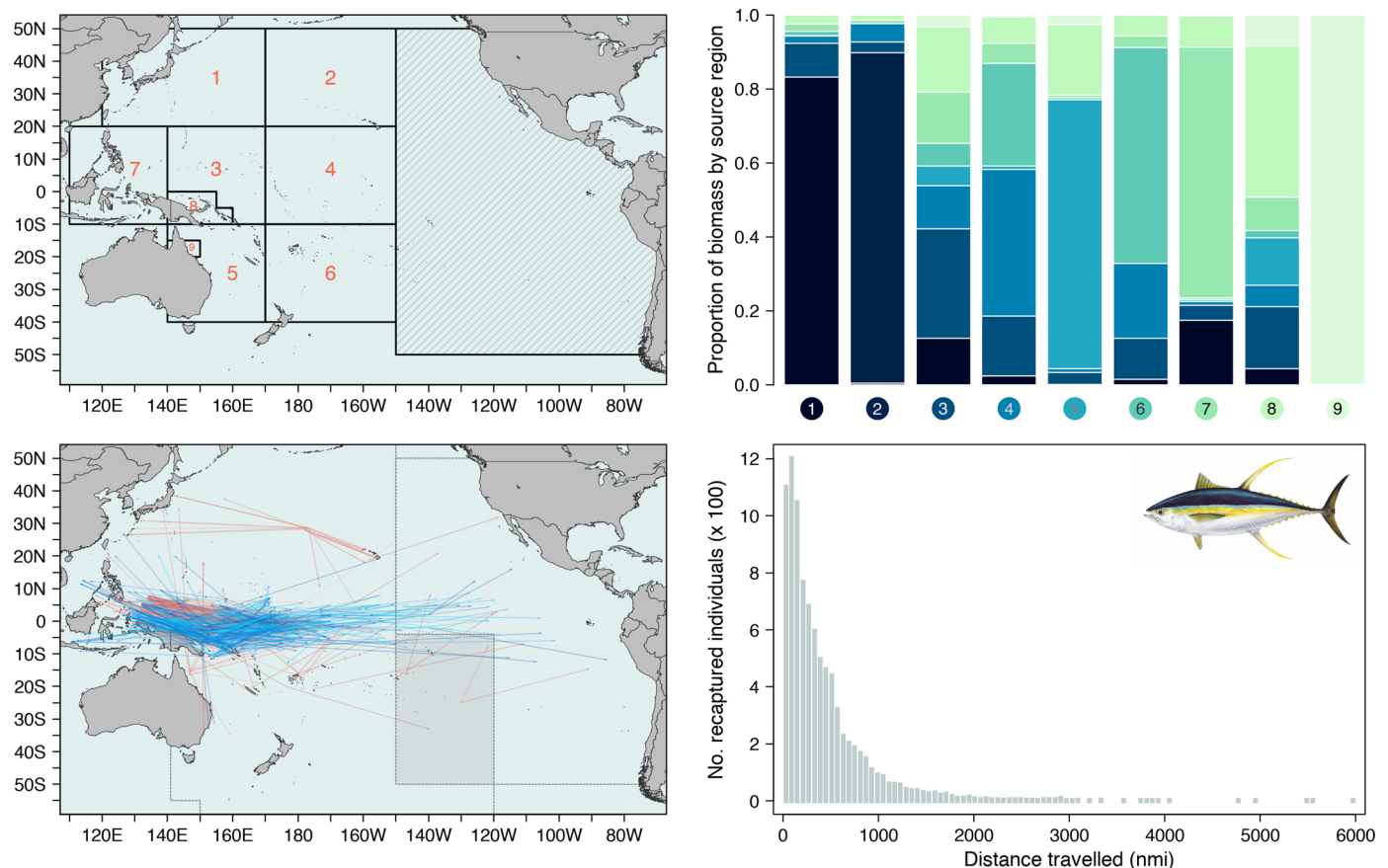


Fig. 3. Top left: The geographic area and regional structure used in the recent stock assessments of yellowfin tuna in the Western and Central Pacific Ocean (WCPO; numbered areas) and Eastern Pacific Ocean (EPO; line shaded area) by Tremblay-Boyer et al. (2017) and Minte-Vera et al. (2019), respectively; bottom left: movements of yellowfin tuna tagged during the Regional Tuna Tagging Programme (RTTP; red arrows) and the Pacific Tuna Tagging Programme (PTTP; blue arrows) recaptured > 1000 nmi from their release point; top right: proportional distribution of total biomass by weight in each WCPO assessment region apportioned by the source regions; bottom right: distribution of observed tag displacements for yellowfin tuna at liberty for ≥ 3 months from RTTP and PTTP data. All tagging data shown are based on SPC holdings. Yellowfin tuna image: Les Hata, © SPC. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

EPO based on the use of allozymes, and Fujino and Kang (1968), who did not observe any significant heterogeneity among samples from the EPO, Hawaii and Kiribati (Line Islands). At a broader spatial scale, significant genetic differentiation between individuals from the WCPO and EPO was first reported by Sharp (1978) at the Glucose Phosphate Isomerase (GPI) locus. Temporal stability of the spatial differentiation observed at the GPI locus was confirmed by Ward et al. (1994). Conversely, Scoles and Graves (1993) found no differences in restriction fragment length polymorphism (RFLP) mtDNA markers between yellowfin tuna from five widely-separated locations in the Pacific Ocean (Australia, Papua New Guinea, Hawaii, Mexico and Ecuador), or between the Pacific Ocean locations and the Atlantic Ocean, which some authors (e.g., Díaz-Jaimes and Uribe-Alcocer, 2006) have proposed may be due to the small sample sizes used. Ward et al. (1997) proposed the existence of distinct WCPO (encompassing Philippines, Coral Sea, Kiribati and Hawaii sampling locations) and EPO (encompassing southern California and northern Mexico sampling locations) populations based on variation within allozymes, but was unable to differentiate WCPO and EPO samples using mtDNA. At a finer spatial scale, Díaz-Jaimes and Uribe-Alcocer (2003) did not observe any significant genetic differentiation in allozymes and Random Amplified Polymorphic DNA (RAPD) markers among yellowfin tuna caught around the Clipperton and Revillagigedo Islands and Baja California. More recently, examination of mtDNA cytochrome c oxidase subunit (COI) suggested the possible existence of sub-populations within the CPO (Li et al., 2015).

Examinations of microsatellite markers have provided varying

results, with some studies (Appleyard et al., 2001; Nomura et al., 2014) unable to demonstrate clear evidence of population differentiation at ocean-wide scales, whereas others have reported observations of differentiation over finer geographical scales. For example, microsatellite markers have been used to differentiate yellowfin tuna from the northern equatorial (Clipperton Islands, Gulf of California, and coastal Mexico) and southern equatorial (Peru) regions of the EPO (Díaz-Jaimes and Uribe-Alcocer, 2006), although the authors note these results may be due to temporal variation in sample collection or non-random sampling. Microsatellite markers also suggest population structuring of yellowfin tuna between the Philippines and the Bismarck Sea, Papua New Guinea (Aguila et al., 2015).

More recently, NGS approaches and SNP markers have been used to investigate population structuring of yellowfin tuna in the Pacific Ocean. Using SNPs, including loci putatively under selection, Grewe et al. (2015) observed population differentiation among samples from the EPO (Baja California), CPO (Tokelau) and WPO (Coral Sea). Pecoraro et al. (2018) identified genetic variation in neutral and potentially adaptive genomic loci between yellowfin tuna caught in the EPO (Mexico) and WCPO (Nauru and Solomon Islands). Sampling on finer geographic scales within the WCPO has not been able to confirm the presence of more than one genetic population from samples collected from yellowfin tuna caught in waters off Australia, Fiji and the Marshall Islands (Evans et al., 2019). In their multidisciplinary study into the stock structure of yellowfin and bigeye tunas in the Indonesian region, Proctor et al. (2019) observed a cline in SNPs in yellowfin tuna

sampled across the Indonesian archipelago, with those in the west more similar to those sampled from the central Indian Ocean and those in the east more similar to those in the WPO. The authors concluded that there was likely to be greater gene flow between fish caught in central Indonesia with the WPO than there was between fish in central Indonesia and the Indian Ocean.

Based on an analysis of SNPs, Anderson et al. (2019a) identified two genetic groupings of yellowfin tuna from samples collected opportunistically from the EEZs of the Federated States of Micronesia (FSM), Kiribati (Gilbert Islands), New Caledonia, and Papua New Guinea in the WPO. They also reported a very high proportion of kin (half- or full-sibling) pairs among yellowfin tuna collected in the same individual sampling events, including between individuals caught at the same FAD than between those caught in the wider EEZ, with most of the individuals identified as kin being sampled from the FSM. Removal of one member of each full-sibling pair resulted in only a single genetic grouping being identified in the samples analysed. From these observations, Anderson et al. (2019a) proposed that yellowfin tuna in association with FADs may remain with related individuals through their first year of life, which may generalise to regional fidelity as adults. The authors cautioned, however, that these observations may result from processes unique to the FSM or the ad-hoc sampling design and, as such, should not be generalised to the broader WCPO. The relatively high levels of heterozygosity and outbreeding reported for the FSM samples are unusual and require further investigation, ideally through the analysis of additional quality-assured DNA samples from this location. Future studies would benefit from structured designs that explicitly consider the spawning dynamics of the species, provide for representative sampling and, importantly, include specific protocols to ensure quality control in tissue sampling and analyses of DNA data. Analyses of kinship relationships may provide a rich source of information that delivers fine-scale resolution of population structure and a more detailed examination of stock dynamics than permitted with current approaches (Bravington et al., 2016; Davies et al., 2016).

2.2.3. Non-genetic studies

Large numbers of predominantly juvenile yellowfin tuna have been tagged in the WCPO using conventional tags through the SSAP, RTTP and PTTP, and other local and regional initiatives. Analyses of tag recoveries indicate that although individual yellowfin tuna are capable of extensive movements, the majority of recaptures have been made close to release sites, suggesting limited movement and a degree of regional fidelity (Fig. 3) (Itano and Williams, 1992; Hampton and Gunn, 1998; Sibert and Hampton, 2003; Fonteneau and Hallier, 2015). For example, in their analysis of conventional tagging returns from activities of the RTTP in the north-west Coral Sea, Hampton and Gunn (1998) observed recaptures as far away as Fiji, Japan, Micronesia, Papua New Guinea and Solomon Islands, suggesting individuals have the potential to mix across their range. The majority of recaptures, however, were in the release area or adjacent Coral Sea (Hampton and Gunn, 1998). Of the tags recovered from yellowfin tuna tagged during the RTTP, ~90 % have been within 1000 nmi of the point of release (SPC unpublished data, cited in Hampton and Gunn, 1998). Sibert and Hampton (2003) estimated yellowfin tuna tagged in the WCPO during the SSAP and RTTP to have a median tagged lifetime displacement ranging from approximately 337–380 nmi. Yellowfin tuna tagged around FADs and seamounts within the Hawaiian archipelago appear to demonstrate high fidelity to these devices and features (Klimley and Holloway, 1999; Itano and Holland, 2000), with observations of tagged fish returning to the site of tagging suggesting that yellowfin tuna may be capable of precise homing (Klimley and Holloway, 1999). Yellowfin tuna has cranial biogenic magnetite, suggesting the presence of a magnetic sense organ (Walker et al., 1984), which may facilitate such behaviour.

Acoustic and archival tags have also been deployed in juvenile

yellowfin tuna across the WPO, and archival tags have been deployed in the CPO as part of the PTTP (SPC-OFF, 2018b). Preliminary analyses of archival tag data support the results from conventional tagging programmes, demonstrating that although some individuals undertake large-scale movements the displacement of most tagged fish is less pronounced (Leroy et al., 2014, 2015). Archival tag returns suggest that small fish tend to move further and that distances travelled increase with time-at-liberty (SPC-OFF, 2015). Modelling of the movement dynamics of yellowfin tuna, based predominantly on the recoveries of tagged juveniles, indicates that movements of fish in the region surrounding Solomon Islands are relatively limited (SPC-OFF, 2017).

Few tagging studies have focused on the movement of adult yellowfin tuna. The only detailed investigation of movement of adult yellowfin tuna in the WCPO to date is that of Evans et al. (2011), who examined data from 20 pop-up satellite archival tags (PSATs) deployed on yellowfin tuna ranging from 135 to 158 cm FL in the northern Tasman Sea and southern Coral Sea. Similar to the results from tagging programmes on juveniles, tagged adult yellowfin tuna showed a limited range of movements (estimated displacements of 54 to 1463 km) with all tagged fish remaining within the Coral and Tasman Seas (Evans et al., 2011). However, the findings were somewhat limited by the relatively short time that tags remained attached (2–168 days).

Results from conventional tagging studies on yellowfin tuna in the EPO suggest that net movements of tagged fish at liberty for more than 30 days tend to be restricted to less than 1000 nmi from their release positions, with little exchange of fish between northern and southern regions (Fink and Bayliff, 1970; Bayliff, 1979, 1984). As a result, Schaefer (2009) concluded that yellowfin tuna from northern and southern areas within the EPO probably represent spatially-segregated sub-stocks. Data from archival tags deployed in the northern EPO indicate that 95 % of tagged fish remained within 1358 km of their release points, with little movement from the northern to the southern regions (Schaefer et al., 2011, 2014).

Variations in life history, morphometrics and meristics have been observed for yellowfin tuna at different spatial scales across the Pacific Ocean. For example, length at 50 % maturity (L_{50}) for female yellowfin tuna differs for fish in the WCPO and EPO, with 95 % confidence intervals around L_{50} ranging from 96.5 to 99.5 cm FL for females in Indonesia and Philippines, 107.2–108.5 cm FL for females in the equatorial western Pacific, 110.1–114.6 cm FL for females caught off Hawaii (Itano, 2000), and 88.6–95.0 cm FL for females in the EPO between 0°N and 20°N (Schaefer, 1998). Latitudinal differences in maturity have been observed in the EPO, with yellowfin tuna maturing at smaller sizes in southern areas (off Costa Rica) than areas to the north (southern Baja California, southern Gulf of California and the Revillagigedo Islands) (Schaefer and Orange, 1956; Orange, 1961). Differences in growth have been observed between fish from Hawaii and the WCPO, although it is unclear whether these differences are due to the existence of separate populations or methodological differences in the preparation and interpretation of otoliths (Farley et al., 2018a). Regional differences in growth have also been predicted from model-based approaches, with yellowfin tuna from Indonesia and Philippines having slower growth rates than those in the wider WCPO (Hoyle et al., 2009). Differences in morphometrics have been observed between yellowfin tuna from Japan, Hawaii, Peru and north-eastern Pacific waters (Godsil, 1948; Godsil and Greenhood, 1951), as well as between French Polynesia, Hawaii and Central America (Schaefer, 1955). Royce (1964) proposed the occurrence of a cline in morphometric characters along the equator from Costa Rica to Micronesia. Schaefer (1991, 1992) demonstrated morphometric and meristic differences among yellowfin tuna from the WPO, CPO and EPO, as well as latitudinal differences for fish from both the WPO and EPO. In the EPO, Schaefer (1992) observed that yellowfin tuna caught off Ecuador have deeper bodies, and have on average one more gill-raker, than those sampled around the

Revillagigedo Islands off the coast of Mexico, indicating limited mixing between groups.

Moore et al. (2019) examined parasite assemblages of juvenile yellowfin tuna collected from locations within Indonesia and two outlier locations in the Indian Ocean and WPO, as part of a larger multidisciplinary study into the stock structure of the species in and adjacent to Indonesia's EEZ (Proctor et al., 2019). Parasite data, and particularly abundances and prevalences of didymozoid species, suggested that little movement of fish occurs from the WPO into the Indonesian archipelago or from the Indonesia archipelago into the eastern Indian Ocean, with the latter observation largely consistent with genetic results (Proctor et al., 2019).

Several studies have used otolith chemistry to investigate hypotheses relating to the origin of sampled populations throughout the WCPO. Gunn et al. (2002) examined elemental concentrations in yellowfin tuna otoliths to investigate the probable origins of fish caught in the western Tasman Sea. Otolith chemistry from the majority of fish caught in the Tasman Sea most closely resembled that of fish originating from the adjacent Coral Sea, rather than fish from other Pacific sampling sites. Combined with the broader understanding of biology, fisheries data, oceanography and tagging, the results suggest that, in some years, yellowfin tuna caught in the Tasman Sea originate predominantly from the Coral Sea, with lower numbers originating from the broader WPO (Gunn et al., 2002).

Wells et al. (2012) examined $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ in otolith cores of young of the year (YOY) yellowfin tuna collected from Hawaii, the Line Islands of Kiribati, Marshall Islands, Philippines, and Solomon Islands and sub-adults (age-1) collected from Hawaii to investigate nursery-specific contribution rates. Mixed-stock analysis revealed that most sub-adults in the Hawaiian fishery had otolith core chemistries representative of nursery areas within Hawaii, with < 10% having core chemistries indicating that they had originated from equatorial nurseries outside Hawaii (Wells et al., 2012).

Using trace elements in addition to stable isotopes, Rooker et al. (2016) reanalysed the same otoliths examined by Wells et al. (2012), along with additional samples from 1 to 2-year-old fish caught in the Marshall Islands. Results suggested that fish caught in Marshall Islands were almost entirely derived from local production, with only a minor contribution of recruits from the central equatorial Pacific, and that all sampled yellowfin tuna from Hawaii originated locally (Rooker et al., 2016).

As part of their multidisciplinary study, Proctor et al. (2019) examined otolith chemistry of yellowfin tuna in and adjacent to Indonesian waters. Patterns in stable isotope and elemental composition indicated fish had not moved large distances in their first six months of life, a result that was consistent with those from examination of parasite assemblages (Moore et al., 2019).

Studies investigating variability in muscle stable isotope ratios suggest limited movement of yellowfin tuna in both the WCPO and EPO. Popp et al. (2007) observed similar latitudinal trends between yellowfin tuna muscle and amino acid $\delta^{15}\text{N}$ values and basal food web $\delta^{15}\text{N}$ values in the EPO, indicating limited movements of individuals in the months leading up to capture. Strong spatial trends in muscle $\delta^{15}\text{N}$ values were also observed by Houssard et al. (2017) for yellowfin tuna in the WCPO, suggesting restricted movement of individuals and high regional residency, at least over the scale of their muscle nitrogen turnover rate (i.e., half-life = 167 days). Enriched size-standardised mercury (Hg) concentrations in muscle of yellowfin tuna at southern latitudes (> 15°S) relative to the equator have also been reported (Houssard et al., 2019), suggesting constrained latitudinal dispersion of fish over the lifetime of these fish.

The most recent stock assessment for yellowfin tuna in the WCPO estimated that biomass in the two northernmost assessment regions (north of 20°N) and in the westernmost assessment region (around Indonesia and the Philippines) results largely from self-recruitment (Fig. 3) (Tremblay-Boyer et al., 2017). Biomass in the two southernmost

regions (south of 10°S) was also estimated to result largely from self-recruitment but with some exchange with the neighbouring equatorial regions (Fig. 3) (Tremblay-Boyer et al., 2017). In contrast, the remaining tropical regions were estimated to have half to two-thirds of their biomass derived from movement of fish that recruited to other regions along the equatorial axis. The same caveats applied to recruitment of skipjack tuna from the assessment model also apply to yellowfin tuna, with potentially low tag reporting rates from tropical tagging programmes in the North Pacific Ocean, as well as fewer tagging data available outside the equatorial region to inform movement (Tremblay-Boyer et al., 2017).

Studies using SEAPODYM suggest that the distribution of yellowfin tuna larvae is strongly contrasted between the WPO and EPO. Large areas of high larval density and seasonally favourable 'hot spots' for spawning are predicted to occur in the Western Pacific Warm Pool around Solomon Islands and Papua New Guinea during the beginning of the third quarter (~July), and within the East China Sea during August–September, with smaller high-density areas occurring in the EPO around Peru and Costa Rica, peaking in March–April (Senina et al., 2015; Lehodey et al., 2017). The model also suggests that in the absence of fishing, slightly stronger rates of transfer occur from Indonesia to Papua New Guinea than in the opposite direction. Papua New Guinea was also identified as a key source of recruits for the WCPO, with the model estimating a 23.6 % reduction in adult biomass in the WCPO when recruitment from Papua New Guinea was removed (Senina et al., 2015).

2.2.4. Synthesis of available information on yellowfin tuna stock structure

The weight of evidence from both genetic and non-genetic studies supports the presence of discrete stocks of yellowfin tuna in the EPO and WCPO, as well as the potential for finer-scale spatial structuring within each of these regions. Analyses of SNPs suggest the occurrence of at least three stocks broadly associated with the WPO, CPO and EPO (Grewé et al., 2015). Further investigation with temporally-repeated samples, quality control of tissue collection, including confirmation of species identification, and consistent application of genetic methods are required to confirm these patterns.

Structuring at finer spatial scales within the WCPO and EPO is less clear. The lack of differentiation of yellowfin tuna caught in waters off Australia, Fiji and the Marshall Islands observed by Evans et al. (2019) suggests that if finer-scale structuring does exist, it occurs at relatively broad geographical scales. In both the WCPO and EPO, tagging data generally suggest limited movement and regional fidelity for the majority of tagged individuals, and support genetic results that indicate limited movement between these two regions. However, as with skipjack tuna, the majority of tagging studies have largely focused on juveniles using conventional tagging approaches in areas of high abundance and concentrated fishing effort, and are constrained by uncertainties around the population representativeness of tagged individuals (see Section 3), limiting resolution of stock boundaries. In the WCPO, information from parasite assemblages (Moore et al., 2019) and otolith chemistry (Gunn et al., 2002; Wells et al., 2012; Rooker et al., 2016; Proctor et al., 2019) also suggest yellowfin tuna do not mix uniformly, although as with tagging studies the majority of these studies have been conducted on juveniles, and are limited by a lack of spatial and temporal replication.

In the EPO, information from tagging (e.g., Fink and Bayliff, 1970; Bayliff, 1979, 1984; Schaefer et al., 2011, 2014), length at maturity (e.g., Schaefer and Orange, 1956; Orange, 1961), muscle stable isotope ratios (Popp et al., 2007) and body morphometrics and meristics (e.g., Schaefer, 1992) suggest spatial structuring between fish in the northern and southern areas. Analyses of DNA microsatellites (Díaz-Jaimes and Uribe-Alcocer, 2006) also support this differentiation, however further studies incorporating larger sample sizes and temporal replicates are required to confirm whether these fish represent different stocks. As such, the actual number of yellowfin tuna stocks present in the Pacific

Ocean, their geographic boundaries, and the mechanisms by which they are structured, remains unresolved.

Assuming data are representative, the limited movement observed for most individual yellowfin tuna from tagging data, together with the observed regional differences in biological parameters, parasite assemblages and otolith chemistry may result in the occurrence of regionally resident populations. However, given their largely continuous distributions in tropical waters of the EPO and WCPO evident from fishery data (IATTC, 2018; Williams and Reid, 2019), and observations of at least some tagged individuals undertaking large-scale movements (e.g., Hampton and Gunn, 1998; Schaefer et al., 2007; SPC-OFP, 2015, 2017; Fig. 3), the occurrence of multiple, fully isolated genetic populations of yellowfin tuna in the Pacific Ocean is unlikely, at least without some additional structuring mechanism, such as fish returning to specific spawning areas. While there is currently no evidence to support such behaviour in Pacific Ocean yellowfin tuna, movements of adult fish, particularly in the WCPO, are poorly understood. In the Atlantic Ocean, trans-basin movements by yellowfin tuna have been proposed to result from fidelity between feeding grounds in the western Atlantic and spawning grounds in the Gulf of Guinea (Bard and Hervé, 1994), however the nature and rate of these hypothesised spawning migrations are yet to be confirmed (Pecoraro et al., 2018). Alternatively, the limited movements displayed by the majority of individuals may result in an isolation by distance structure, particularly if individuals reproduce with their nearest neighbours. Supporting this hypothesis is the observation of a cline in genetic structure from SNP markers in yellowfin tuna across sampling locations in the Indian and far western Pacific Oceans by Proctor et al. (2019). Further studies are required to test these various hypotheses.

2.3. Bigeye tuna

2.3.1. Relevant biology and spatial considerations in stock assessment approaches

Bigeye tuna are broadly distributed across the Pacific Ocean, inhabiting tropical to temperate waters from approximately 45°N to 40°S in the WCPO, and from approximately 40°N to 30°S in the EPO (Calkins, 1980). On the basis of gonad condition of mature fish and observed distributions of larvae, spawning of bigeye tuna is considered to occur year-round in tropical equatorial waters of the Pacific Ocean and seasonally in subtropical waters when water temperatures exceed 24°C (Schaefer, 2001b; Schaefer et al., 2005). Farley et al. (2017) observed spawning capable females between 12°N and 12°S and between 137°E and 130°W, in water temperatures between 27.7°C and 30.3°C, suggesting central equatorial waters may be an important spawning region for bigeye tuna. Nishikawa et al. (1985) suggested that the region between Japan and the Philippines is a particularly important spawning area for bigeye tuna in the WPO, with spawning occurring there during spring and early summer. Aggregations of bigeye tuna in the north-western Coral Sea have been associated with spawning (McPherson, 1988; Farley et al., 2003). In the EPO, Schaefer et al. (2005) observed spawning across a wide area spanning approximately 15°N and 15°S to 105°W to 175°W.

The most recent stock assessment for bigeye tuna in the WCPO incorporated a 9-region structure across the area 40°S–50°N (Fig. 4). This spatial structuring was informed by the nature of the operating fleets (longline vessels targeting larger individuals and operating primarily in more temperate waters, and purse-seine vessels catching smaller individuals and operating almost exclusively in equatorial waters) and tag mixing assumptions, with additional division of areas along the longitudinal axes (McKechnie et al., 2014, 2017a). Shifting the northern edge of the equatorial region from 20°N to 10°N suggested the assessment could be sensitive to the configuration of regional structure (McKechnie et al., 2017b; Vincent et al., 2018). The most recent assessment for bigeye tuna in the EPO did not explicitly include regional structuring but, similar to the assessments of yellowfin tuna, adopted a

‘fleets-as-areas’ approach (Xu et al., 2018). Schaefer (2009) observed that bigeye tuna are caught primarily in two distinct areas in the EPO, a southern area between 10°N and 20°S from coastal waters to 150°W, and a northern area between about 15°N and 35°N from 130°W to 150°W.

A Pacific-wide assessment for bigeye tuna encompassing both the WCPO and the EPO was conducted in 2015 and included regional spatial structuring that matched the WCPO and the EPO assessments at the time. This assessment assumed ‘EPO-style’ growth patterns (see Section 2.3.3. below) across the Pacific Ocean. The resulting estimates of stock status of WCPO bigeye tuna from the Pacific-wide model were not substantially different from those estimated using the WCPO-only model, so it was concluded that conducting separate assessments in the WCPO and EPO was appropriate (McKechnie et al., 2015).

2.3.2. Genetic studies

To date, the majority of studies using allozymes, mtDNA and microsatellites have not observed evidence of spatial structuring in bigeye tuna from differing locations in the Pacific Ocean, or between Pacific Ocean and Indian Ocean sampling locations (Fujino and Kang, 1968; Alvarado Bremer et al., 1998; Chow et al., 2000; Wu et al., 2014). Many of these studies have suggested that a lack of structuring is consistent with broad-scale panmixia among bigeye tuna in the region but also recognise that additional sampling and alternative techniques may be required to further investigate population structure (Fujino and Kang, 1968; Alvarado Bremer et al., 1998; Chow et al., 2000; Wu et al., 2014). However, Grewe and Hampton (1998) found some evidence for restricted gene flow between the Philippines and Ecuador, their two most widely separated sampling areas. The ability to further differentiate populations, however, was limited by small sample sizes. Grewe and Hampton (1998) recommended that larger sample sizes and examination of additional loci would be needed to adequately determine the population structure of bigeye tuna in the Pacific Ocean.

Examination of SNPs by Proctor et al. (2019) from bigeye tuna sampled across the Indonesian archipelago and two outlier locations in the Indian and Pacific Oceans revealed a cline in genetic structure across sampling locations consistent with an isolation by distance model. Their results suggested restricted connectivity between the Indian Ocean and WPO sampling locations, with the central Indonesian sites appearing to have limited connectivity to both areas. These conclusions were largely consistent with analyses of otolith chemistry and parasite assemblages in the same study (see Section 2.3.3).

2.3.3. Non-genetic studies

Large numbers of bigeye tuna have been tagged across the Pacific Ocean. The bulk of tagging studies however, particularly in the WCPO, have focused on juveniles and sub-adults, typically less than 70 cm FL (Leroy et al., 2015). Recaptured bigeye tuna marked with conventional tags across the WCPO have revealed a range of movements, with some individuals dispersing large distances (Fig. 4). However, the vast majority of fish tagged with conventional tags have been recaptured less than 1000 nmi from their release points (Fig. 4) (Miyabe, 1994; Hampton and Gunn, 1998; Itano and Holland, 2000; Gunn et al., 2005).

Recaptures of predominantly juvenile bigeye tuna conventionally tagged at the 140°W, 155°W, 170°W and 180° meridians in the CPO and at liberty for between 30 and 1701 days were mainly within approximately 1000 nmi of their original release point, and within 10° of latitude from the equator, suggesting a high degree of regional residency and constrained latitudinal dispersion (Schaefer et al., 2015). Dispersal, where it did occur, was primarily eastwards, and there was substantial mixing of bigeye tuna between release longitudes (Schaefer et al., 2015). Bigeye tuna (predominantly < 80 cm FL) tagged around FADs and seamounts within the Hawaiian archipelago have been shown to demonstrate high fidelity to these features (Itano and Holland, 2000).

Archival tagging studies conducted in the WCPO (primarily on

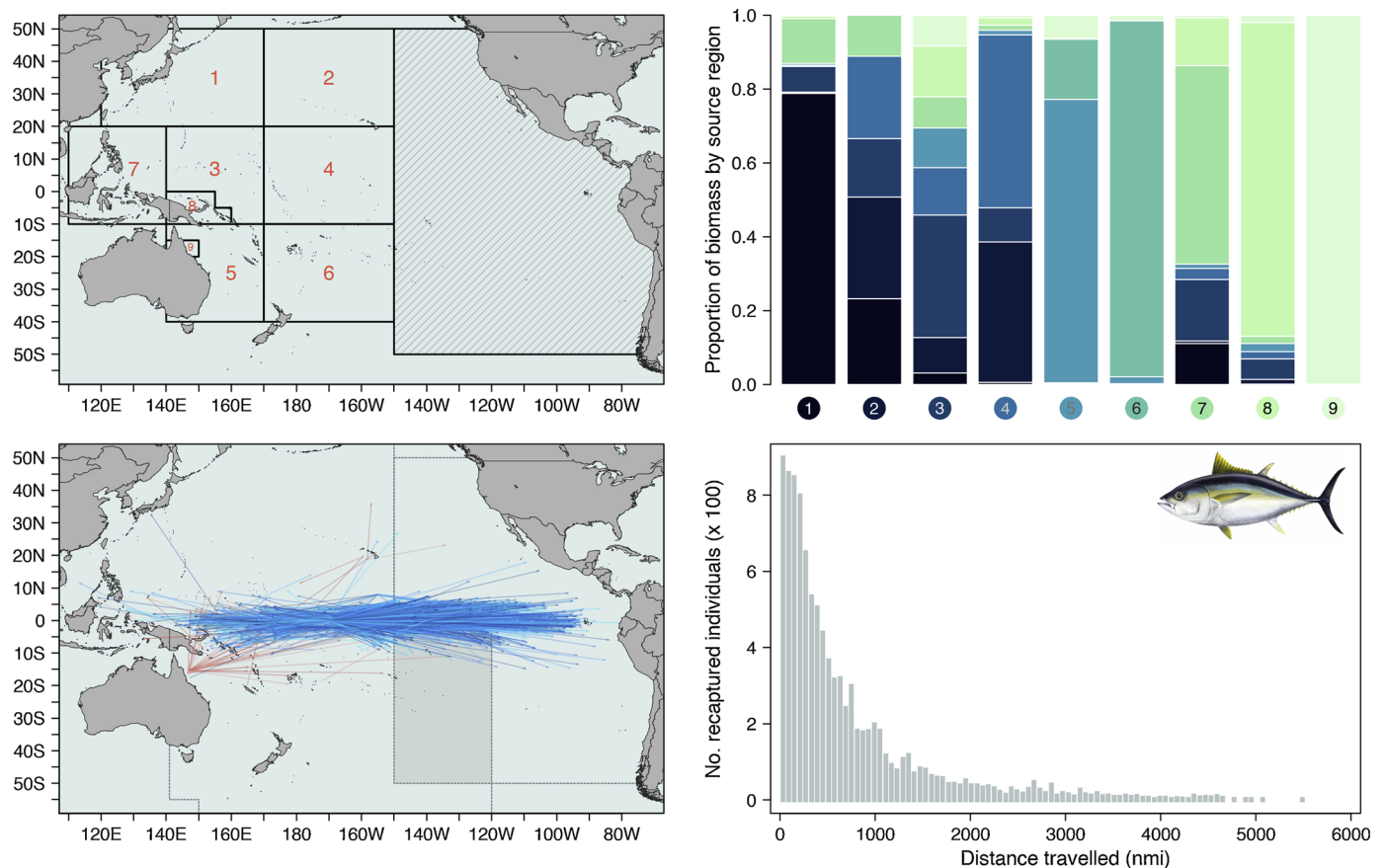


Fig. 4. Top left: The geographic area and regional structure used in the recent stock assessments of bigeye tuna in the Western and Central Pacific Ocean (WCPO; numbered areas) and Eastern Pacific Ocean (EPO; line shaded area) by [McKechnie et al. \(2017a\)](#) and [Xu et al. \(2018\)](#), respectively; bottom left: movements of bigeye tuna tagged during the Regional Tuna Tagging Programme (RTTP; red arrows) and the Pacific Tuna Tagging Programme (PTTP; blue arrows) recaptured > 1000 nmi from their release point; top right: proportional distribution of total biomass by weight in each WCPO assessment region apportioned by the source regions; bottom right: distribution of observed tag displacements for bigeye tuna at liberty for ≥ 3 months from RTTP and PTPP data. All tagging data shown are based on SPC holdings. Bigeye tuna image: Les Hata, © SPC. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

juveniles) support the findings of conventional tagging programmes. Bigeye tuna tagged in the Coral Sea demonstrated local residence, cyclical movements between the Coral Sea and the broader WPO, and potentially broad-scale longitudinal dispersal eastwards into the wider WCPO ([Gunn et al., 2005](#); [Evans et al., 2008](#)). [Gunn et al. \(2005\)](#) hypothesised that the cyclical movement observed for bigeye tuna in the northwest Coral Sea may be linked in part to movements from spawning sites and into areas of the Coral Sea and WPO at the completion of spawning. Bigeye tuna tagged with archival tags in the Bismarck and Solomon Seas were also observed to undertake limited movements over their time at liberty ([Leroy et al., 2014](#); [Abascal et al., 2018](#)). Results from archival tagging studies on fish generally < 100 cm in length in the CPO show similar patterns of movement to that derived from conventional tagging, demonstrating constrained latitudinal dispersal, some regional fidelity, substantial mixing of bigeye tuna between release locations, particularly between adjacent areas, as well as some extensive eastward longitudinal movement, particularly in those fish tagged at 140°W and 170°W ([Schaefer et al., 2015](#)).

Regional fidelity and limited latitudinal movement has also been observed in conventionally-tagged bigeye tuna released in the equatorial EPO ([Schaefer and Fuller, 2009](#)). Bigeye tuna tagged between 95°W and 97°W that were at liberty for between 31 to 2291 days were predominantly recaptured within approximately 1000 nmi of their original release point with limited latitudinal displacement ([Schaefer and Fuller, 2009](#)). Dispersal of fish tagged was predominantly westward in nature and the distance dispersed appeared to be positively related to

fish size and time at liberty ([Schaefer and Fuller, 2009](#)). Regional fidelity has also been observed from archival tag deployments on bigeye tuna in the EPO, with restricted westward movements ([Schaefer and Fuller, 2009](#)). Notably, of the 96 recaptures of archivally-tagged bigeye tuna tagged in the EPO analysed by [Schaefer and Fuller \(2010\)](#), one individual that was at liberty for 4.1 years undertook two very similar cyclical movements during its third and fourth years at liberty, moving into the CPO between ~150°W and ~160°W in November–December, before returning to ~84°W in early May in each year.

On the basis of archival tagging data from the equatorial WPO, CPO and EPO, [Schaefer et al. \(2015\)](#) proposed that bigeye tuna demonstrated three types of movement behaviours: i) fish that are residents within an area (<1000 nmi of release location), ii) fish that are residents, yet undertake cyclical excursions outside the area of residency, and iii) fish that are nomadic and do not demonstrate type 1 or type 2 movement patterns. They further proposed, based on the degree of mixing observed in association with these behaviours, the existence of three putative stocks of bigeye tuna in the equatorial Pacific Ocean – eastern, central, and western stocks – with stock boundaries at about 120°W and 180°, and constrained between 10°N and 10°S. On the basis of constrained latitudinal movement evident in each region, they suggested that there was potential for the existence of six additional stocks; three northward and three southward of the equatorial stocks.

Spatial analysis of length-at-age data suggests that there are differences in growth of bigeye tuna within the Pacific Ocean, indicating that mixing is not uniform. [Farley et al. \(2017\)](#) identified four broad

areas in the WCPO with differing growth profiles, corresponding roughly to areas i) west of $\sim 140^\circ\text{E}$ (encompassing Indonesia and the Philippines), ii) east of $\sim 140^\circ\text{E}$ to $\sim 150^\circ\text{W}$ and north to $\sim 5^\circ\text{N}$, iii) north of 5°N , and iv) east of $\sim 150^\circ\text{W}$ (encompassing French Polynesia samples), with fish from the westernmost ($< 140^\circ\text{E}$) and easternmost ($\sim 155^\circ\text{W}$ – 130°W) areas of the sampling region observed to grow faster compared to those from central longitudes (Farley et al., 2017, 2018b). However, the authors cautioned that the data were limited both spatially and by length/age coverage and that further work was necessary to fully explore spatial variation in growth across the Pacific Ocean. Examination of otolith weight-at-length data over a broader area revealed similar spatial patterns with larger length-at-otolith weight occurring east of $\sim 130^\circ\text{W}$ (Farley et al., 2018b). This is consistent with faster growth rates observed in bigeye tuna from the EPO (Schaefer and Fuller, 2006). There is ongoing work to clarify whether the differences in growth between the WCPO and EPO is due to the existence of separate stocks or methodological differences in the preparation and interpretation of otoliths (Farley et al., 2018b). Spatial differences in length at maturity have also been observed, with mean length at 50 % maturity of females estimated to be $\sim 103\text{ cm}$ in the WPO, $\sim 108\text{ cm}$ in the CPO and 135 cm FL in the EPO (Schaefer et al., 2005; Zhu et al., 2010; Sun et al., 2013; Farley et al., 2017).

Studies investigating variability in parasite assemblages or otolith chemistry in bigeye tuna in the Pacific have been limited. Moore et al. (2019) examined the parasite fauna of juvenile bigeye tuna collected from locations within the Indonesian EEZ and two outlier locations – Maldives and Solomon Islands – as part of the multidisciplinary study of Proctor et al. (2019). Their results suggested little movement of juvenile bigeye tuna between Indonesia waters and the two outlier locations, from the WPO sites into the Indonesian archipelago, or from the Indonesia archipelago to the eastern Indian Ocean. These results were largely consistent with otolith isotope and elemental composition data, which suggested that fish had not moved very far in their first few months of life (Proctor et al., 2019).

Comparisons of stable isotopes ($\delta^{13}\text{C}$ and $\delta^{18}\text{O}$) and chemical signatures of the natal regions of otoliths from young of the year bigeye tuna collected from four regions throughout the WCPO have revealed spatial variability in these isotopes, particularly in the depletion of $\delta^{18}\text{O}$ (Rooker et al., 2016). When compared with the stable isotope and chemical signatures of natal regions of otoliths from 1 to 2-year-old bigeye tuna from the Marshall Islands and Hawaii, Rooker et al. (2016) concluded that bigeye tuna from the Marshall Islands were derived almost entirely from local production, with a minor contribution of recruits from the central equatorial Pacific. In contrast, a large proportion of bigeye tuna caught off Hawaii were deemed to have originated from the central equatorial region (Rooker et al., 2016).

Examination of the stable isotopes of muscle tissue from bigeye tuna also suggests some spatial structuring of individuals. Houssard et al. (2017) observed strong spatial trends in $\delta^{15}\text{N}$ values for bigeye tuna sampled across the WCPO, suggesting restricted movement of individuals and a degree of regional residency, at least over the scale of their muscle nitrogen turnover rate (i.e., half-life = 167 days). Spatial variation in Hg concentrations of bigeye tuna muscle have also been documented, with Houssard et al. (2019) observing enriched size-standardised Hg concentrations in fish caught in southern latitudes ($> 15^\circ\text{S}$) relative to those caught from the equator, and comparably higher (size-standardised) Hg concentrations in fish caught off Tonga and Fiji than those caught at comparable latitudes in French Polynesia.

The most recent stock assessment for bigeye tuna in the WCPO estimated some north-south exchange between equatorial regions and the North Pacific Ocean, as well as movement of recruits from west to east in the North Pacific (Fig. 4). The same general trend that occurs for yellowfin tuna is otherwise predicted, i.e., mixing throughout the equatorial regions but with higher retention of recruits in the westernmost tropical region. Bigeye tuna in the southernmost assessment regions were estimated to result mostly from self-recruitment, with a

small proportion of recruits predicted to move from west to east (Fig. 4) (McKechnie et al., 2017a).

Applications of SEAPODYM estimate an optimum mean spawning temperature of 26.8°C for bigeye tuna, resulting in peak larval distributions between 26° to 28°C (Lehodey et al., 2018). As a result, model outputs predict a large spawning area in the central equatorial region, with juvenile bigeye tuna concentrated mainly in the wider tropical CPO, and adults extending from this zone into more temperate latitudes following the Kuroshio Current Extension to the north and East Australian Current to the south. Bigeye tuna movement parameters appear to have varied considerably across parameter optimisations (Lehodey et al., 2018; Senina et al., 2018), suggesting very low to moderate diffusion in response to habitat quality, potentially affecting mixing.

2.3.4. Synthesis of available information on bigeye tuna stock structure

The stock structure of bigeye tuna in the Pacific Ocean remains unresolved. Genetic studies for the most part have provided little evidence of significant structuring between the EPO and WCPO, with only Grewe and Hampton (1998) indicating potential restricted gene flow between the far WPO and far EPO. However, genetic studies conducted to date have been limited by sampling design effects, including limited sample sizes, and a comprehensive assessment using NGS approaches across the Pacific Ocean has yet to be conducted. Finer-scale structuring is similarly unclear. Observations from tagging studies suggest a degree of regional fidelity in both the EPO and WCPO, some extensive eastward longitudinal dispersion (particularly in the WPO and CPO), constrained latitudinal movement and the likely occurrence of spatial structuring of bigeye tuna stocks between the EPO, CPO and WPO (e.g., Schaefer et al., 2015). However tagging studies conducted to date have been limited by relatively low numbers of recaptures, time at liberty of individuals, varying tag reporting rates, and uncertainties around the population representativeness of tagged individuals (see Section 3), precluding resolution of stock boundaries. Observations of regional differences in growth and reproductive biology (Farley et al., 2017, 2018b) support the differentiation of fish from the EPO and WCPO, and finer-scale patterns, where available, are consistent with the occurrence of regional fidelity. Available otolith chemistry data (Rooker et al., 2016) appear to contrast with the observation of constrained latitudinal dispersion of bigeye tuna within central equatorial waters evident from tagging data, potentially indicating that the dispersal evident from otolith chemistry may have occurred when fish were at younger ages than those of tagged individuals. Structured sampling programmes are required to test this hypothesis. More broadly, information on otolith chemistry (e.g., Rooker et al., 2016; Proctor et al., 2019) and parasite assemblages (e.g., Moore et al., 2019) suggest bigeye tuna do not mix uniformly, but as with those conducted on yellowfin tuna, these studies are life-stage specific, and have been limited by a lack of spatial and temporal diversity. As such, the spatial resolution of bigeye tuna stocks across the Pacific Ocean is poorly understood, and warrants further investigation.

As with yellowfin tuna, the largely continuous distribution of bigeye tuna in tropical waters of the EPO and WCPO evident from fishery data (IATTC, 2018), and observations of individuals undertaking large-scale movement from tagging studies (e.g., Hampton and Gunn, 1998; Schaefer et al., 2015; SPC-OF, 2015, 2017; Fig. 4), indicate that the occurrence of multiple, fully discrete, closed populations of bigeye tuna in the Pacific Ocean is unlikely, at least without some additional structuring mechanism, such as fish returning to specific spawning areas (see Section 3). Although there is no direct evidence of fidelity to spawning areas in bigeye tuna, the hypothesis of Gunn et al. (2005), who proposed that the small numbers of cyclical movements observed in bigeye tuna in the northwest Coral Sea may be linked in part to movements from spawning sites and into more dispersed areas of the Coral Sea and WPO at the completion of spawning, is consistent with spawning area fidelity, at least for a proportion of the population.

Similar cyclical movements have also been observed in an individual bigeye tuna tagged in the EPO (Schaefer and Fuller, 2010). Alternatively, limited movements may result in stock structure via isolation by distance, particularly if individuals reproduce with their nearest neighbours. The observed cline in genetic structure in bigeye tuna across sampling locations spanning the Indian Ocean and far WPO by Proctor et al. (2019) is consistent with an isolation by distance hypothesis, although additional studies are required to assess whether this pattern is demonstrated by the species more broadly across its Pacific Ocean distribution. The similarity of these results with those of yellowfin tuna suggest a common underlying biogeographic mechanism that restricts genetic connectivity at ocean basin scales. The observation of Schaefer et al. (2015) that the greatest amount of mixing of tagged bigeye tuna occurs between adjacent areas is also broadly consistent with an isolation by distance model. Further sampling is required to test these various hypotheses.

2.4. South Pacific albacore tuna

2.4.1. Relevant biology and spatial considerations in stock assessment approaches

Albacore tuna are widely distributed in the Pacific Ocean between approximately 50°N and 40°S, although fisheries catch and tagging data suggest limited occurrence in equatorial waters between 5°N and 5°S (Lewis, 1990; Williams et al., 2012; Nikolic et al., 2017). Historically, two stocks have been recognised in the Pacific: a North Pacific Ocean stock and a South Pacific Ocean stock. However, several recent genetic studies report apparent homogeneity of fish caught in the northern and southern hemispheres (e.g., Montes et al., 2012; Albaina et al., 2013), casting some doubt on the existence of separate stocks.

In contrast to skipjack, yellowfin and bigeye tunas, South Pacific albacore tuna have a relatively discrete spawning season, with spawning occurring in tropical and sub-tropical waters exceeding 24 °C between 10°S and 25°S between September and May, with a peak between October and December (Ramon and Bailey, 1996; Farley et al., 2013). Juveniles are thought to move south from their spawning grounds into surface waters around New Zealand and in the vicinity of the subtropical convergence zone in the central Pacific, where they are caught by longline and troll-fisheries at around one year old. As they age, South Pacific albacore tuna gradually disperse into lower latitudes north of 30°S (Langley, 2004, 2006; Langley and Hampton, 2005), where they are primarily caught by longline fleets. Longline catch data indicate that adult South Pacific albacore tuna may migrate seasonally between tropical and subtropical waters, moving south during early summer, and north during winter, coincident with the seasonal shift in the 20–28 °C sea surface temperature isotherm (Langley, 2004, 2006; Langley and Hampton, 2005). Spatial variability in maturity at age and muscle fatty acid composition support the latitudinal separation of age groups evident from the size distribution of fisheries catches (Farley et al., 2014; Parrish et al., 2015).

Although South Pacific-wide assessments for the species have been performed historically, the most recent stock assessment for South Pacific albacore tuna incorporated a 5-region structure in the area from 50°S to the equator between 140°E and 150°W, and from 50°S to 5°S between 150°W and 130°W (Fig. 5) (Tremblay-Boyer et al., 2018). This region corresponds closely to the WCPFC Convention Area south of the equator. The eastern Pacific component of the stock has not been included in recent assessments, due to low catches and poor data quality, although increasing catches in this region have resulted in requests for a Pacific-wide assessment of the species (Pilling and Brouwer, 2018). Spatial structuring of the assessment model used in the WCPO has varied through time with the structure informed by biological hypotheses of seasonal movement, spatial structuring of the population by age, and patterns of fishing activity. The distribution of recruitment was constrained to the southernmost regions in the most recent assessment based on the distribution of newly-recruited fish in the catch,

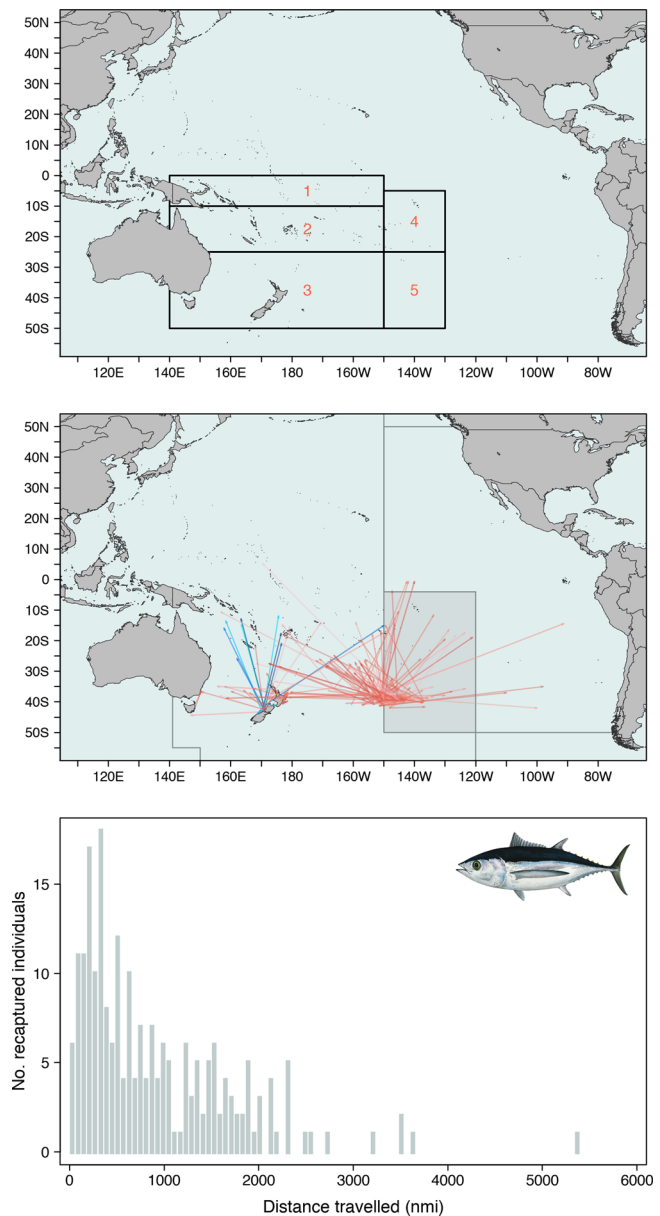


Fig. 5. Top: The geographic area and regional structure used in the recent stock assessment for South Pacific albacore tuna in the Western and Central Pacific Ocean (WCPO; numbered areas) by Tremblay-Boyer et al. (2018); middle: movements of tagged albacore tuna tagged during the Regional Tuna Tagging Programme (RTTP; red arrows) and the South Pacific Albacore Tagging Programme (SPATP; blue arrows); bottom: distribution of observed tag displacements for albacore tuna at liberty for ≥ 3 months from RTTP and SPATP data. All tagging data shown are based on SPC holdings. Note predictions of total biomass distributions are not available from the assessment model (see text). Albacore tuna image: Les Hata, © SPC. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

precluding model predictions on regional sources of recruitment to adult biomass (Tremblay-Boyer et al., 2018).

2.4.2. Genetic studies

Few studies have used molecular approaches to examine the presence of population structuring within South Pacific albacore tuna. Differences in DNA microsatellites have been reported between albacore tuna in the WPO (Australia) and EPO (Chile and Peru) (Takagi et al., 2001), and the WPO (between New Caledonia and Vanuatu) and CPO (French Polynesia) (Montes et al., 2012). In contrast, Davies et al.

(2011) found no differentiation of microsatellites between samples from New Caledonia and French Polynesia. Analyses using SNPs have also yielded potentially contrasting results. Laconcha et al. (2015) found little evidence to indicate differentiation in SNPs between samples from New Caledonia and French Polynesia, or between these locations and the North Pacific Ocean. Anderson et al. (2019b) found no evidence to support the presence of genetic variability in South Pacific albacore tuna from four sampling areas in the WPO and CPO (French Polynesia, New Caledonia, New Zealand and Tonga) at neutral SNP loci. They reported observations of greater potential structure at adaptive SNP loci, with samples from French Polynesia differentiated from those sampled at locations to the west. The authors advise caution in the interpretation of their results, noting that it is unclear to what extent spatial or temporal differences in sampling strategies might have contributed to their observations. Preliminary analyses of SNPs from samples collected from finer geographic scales within the WCPO has not been able to confirm the presence of more than one genetic population from albacore tuna collected off Australia, New Caledonia and New Zealand (Evans et al., 2019).

2.4.3. Non-genetic studies

Albacore tuna are more challenging to tag than skipjack, yellowfin and bigeye tunas, largely because many of the fish do not survive the longline capture process (the predominant method by which they are caught). As a result, comparatively few conventionally-tagged albacore tuna have been released in the Pacific Ocean. Nevertheless, some tagging of South Pacific albacore tuna has been undertaken to inform stock assessments for this species with respect to growth, movement, and mortality, with tagging operations having been conducted primarily south of 35°S, and predominantly on juveniles. Although recaptures have been low (~1 % of tagged fish), the information derived supports connectivity of fish between high and low latitudes, and highlights the potential for individual fish to undertake long-range latitudinal and longitudinal dispersion, with some individuals being recaptured several thousands of kilometres from their release sites (Fig. 5) (Labelle and Hampton, 2003; SPC-OFP, 2017, 2018b). There have been 19 pop-up satellite archival tags deployed on South Pacific albacore tuna, in the waters of New Caledonia, New Zealand and Tonga (Williams et al., 2015). Although the durations of these tag deployments were limited (≤ 50 days), displacements varied between release sites. Fish tagged in New Zealand waters moved greater distances than those tagged in New Caledonia and Tonga (Williams et al., 2015).

Spatial variability in growth has been reported within South Pacific albacore tuna, with both females and males reaching greater length-at-age at easterly than at westerly longitudes (Williams et al., 2012). Longitudinal differences have also been observed in gonad development, with mature albacore tuna in the east having heavier gonads in relation to their length than those in the west (Farley et al., 2013). Together, these results suggest some structuring of individuals at broad spatial scales within the WCPO.

Jones (1991) examined parasite assemblages of albacore tuna across the south-western Pacific. Based on the abundances of 10 species of didymozoid, he concluded that fish moved south from the tropics to New Zealand and then returned north to spawn with the onset of sexual maturity, a result that is consistent with tagging and fishery catch data. In addition, there was evidence to suggest that fish were also moving longitudinally along the subtropical convergence zone.

Examination of the otolith chemistry of South Pacific albacore tuna has been limited to one study by Macdonald et al. (2013). They investigated chemical signatures at the natal region of otoliths from fish (80–95 cm FL) captured around New Caledonia, New Zealand and French Polynesia. Albacore tuna caught off New Caledonia and New Zealand had similar chemical signatures, suggesting that they originated from areas of similar water chemistry. In contrast, those from French Polynesia were significantly different, suggesting they had originated from a separate larval source. Although the locations of larval

origins were not identified, these results demonstrate the potential for some degree of spatial structuring of spawning populations of albacore tuna within the South Pacific (Macdonald et al., 2013).

Spatial patterns in Hg concentrations of albacore tuna muscle have also been reported. Houssard et al. (2019) observed enriched size-standardised Hg concentrations in fish caught in southern latitudes (~15°S–25°S) relative to those caught north of 15°S. However, these results were limited by the restricted size range of fish sampled and the narrow latitudinal band the samples were collected from, precluding conclusions as to whether the observed patterns were a result of fish size or location.

Applications of SEAPODYM estimate an optimal spawning SST for South Pacific albacore tuna of 28 °C, with the northward spawning migration peaking in early May (Senina et al., 2018). Optimal temperatures for foraging habitats for the species were estimated as ranging from 11.8–23.5 °C. Little evidence on connectivity and stock structure *per se* is available from SEAPODYM, with the model estimating broad-scale movement of albacore tuna corresponding with seasonal shifts of the 23° to 28 °C SST isotherm location (Senina et al., 2018).

Fishery data indicate that catch rates tend to be lower in EEZs of those PICTs where fishing effort is highest, and higher in the EEZs of PICTs where fishing effort has been lower (Brouwer et al., 2019), suggesting the possible occurrence of regional fidelity of adults.

2.4.4. Synthesis of available information on South Pacific albacore tuna stock structure

The most recent stock assessment for South Pacific albacore tuna (Tremblay-Boyer et al., 2018) assumes the boundary of the stock extends from the east coast of Australia to 130°W. This model structure assumes that South Pacific albacore tuna east of 130°W are a separate stock. However, it is not clear whether the boundaries of the model domain reflect the underlying population structure of South Pacific albacore tuna. Microsatellite DNA analyses (Takagi et al., 2001) support the separation of fish from the southwest and southeast Pacific, although the boundary between these putative stocks, and number of additional stocks between these widely-spaced areas, is unknown. Within the assessment area, DNA microsatellites (Montes et al., 2012) appear to contrast the current single stock paradigm, suggesting the possible occurrence of at least two genetic stocks. These results are potentially supported by separate analyses of adaptive SNP loci (Anderson et al., 2019b). Biological (Williams et al., 2012; Farley et al., 2013) and otolith chemistry (Macdonald et al., 2013) data further support these findings, with those individuals caught in the far eastern regions of the stock assessment area demonstrating biological characteristics and otolith core chemistries that vary from those in the western regions of the assessment area. However, such studies have been limited by a general lack of spatial and temporal resolution and structured sampling. Recoveries of tagged fish indicate the potential for individuals to undertake long-range latitudinal and longitudinal dispersion, potentially resulting in stock mixing. The majority of tagging, however, has been conducted on individuals south of ~35°S, and thus predominantly on juveniles. Further sampling is required to quantify the actual number of stocks present and their geographic boundaries, both within and beyond the current spatial domain used for stock assessment.

The latitudinal ontogenetic movement of South Pacific albacore tuna, coupled with more limited longitudinal dispersal of adults, may facilitate the maintenance of regionally resident groups of adults in the South Pacific Ocean, with genetic linkages potentially maintained at varying spatial scales by larval dispersal and/or longitudinal movements of juveniles along the subtropical convergence zone. The observed longitudinal differences biological and fishery catch rate data are consistent with expectations from regional residency of adults. Alternatively, limited longitudinal movements may result in an isolation by distance structure, particularly if individuals reproduce with their nearest neighbours, or tend towards a metapopulation structure

should larvae and/or juveniles disperse and mix among largely resident adult populations. There is currently limited evidence to support or refute either of these two scenarios. Broad-scale spawning area fidelity appears unlikely for South Pacific albacore tuna, as there is no evidence of specific spawning areas for the species, although individual fish may return to specific spawning sites. Further studies are warranted to explore these various hypotheses.

3. Main uncertainties and future directions to understanding the stock structures of skipjack, yellowfin, bigeye and South Pacific albacore tunas in the Pacific Ocean

Recent studies across the Pacific Ocean have resulted in increased knowledge of the spatial dynamics of the four tuna species reviewed here. They identify the potential for varying degrees of spatial structuring of stocks, rather than panmixia, for each species. However, from available data, it is currently not possible to define the stock structure of any of the four tuna species at scales relevant to regional management. This is because most studies have typically been constrained by effects of scale (both spatial and temporal), sampling design, limitations in resolution of the techniques, availability of samples or data and, potentially, the behaviour of the tuna species themselves. For example, although a large amount of tagging data exists, particularly for skipjack and yellowfin tunas, most tagging studies have focused on juvenile fish tagged with conventional tags, and have been spatially limited, with releases conducted mainly in areas of high abundance and concentrated fishing effort. This is partly because these studies were not designed solely to provide information on stock structure, but to assess a range of parameters for use in stock assessments, including movement and mixing, estimations of growth rates, natural and fishing mortality, and abundance (Leroy et al., 2015). Furthermore, inferences of stock structure based on movement and mixing from conventional tagging studies are inherently limited by the point-to-point nature of the resulting data, with no information on the movement of fish between release and recovery, as well as the number of recaptures (particularly for South Pacific albacore tuna), time of individuals at liberty, the distribution of tagging and recapture effort, varying tag reporting rates, and uncertainties around the population representativeness of tagged individuals (Hunter et al., 1986; Leroy et al., 2015; Evans et al., 2016).

Genetic studies conducted to date have largely proven inconclusive in resolving the stock structure of the four tuna species. Historically, most genetic studies on Pacific tuna populations have used a small number of markers distributed in a limited portion of the genome (Appleyard et al., 2001), that are extremely sensitive to the movement of small numbers of individuals between populations (Slatkin, 1987), or that show low levels of genetic differentiation resulting from large population sizes and high fecundity (Palumbi, 2003; Ely et al., 2005), such as estimated for skipjack, yellowfin, bigeye and South Pacific albacore tunas. Elsewhere, studies have been limited by sampling design and logistical issues, including sample size limitations; opportunistic sampling of fish on fishing grounds, which may include a mix of several stocks, to identify discrete reproductive units; a lack of structured sampling; or by widely-separated sampling locations (Richardson, 1983; Grewe and Hampton, 1998; Grewe et al., 2015; Pecoraro et al., 2018; Anderson et al., 2019a, b). Studies employing biochemical analyses (e.g., otolith or muscle chemistry), parasites, morphometrics and meristics have yielded informative results but have been limited by the spatial and temporal scales over which such studies have operated and/or a lack of structured sampling.

Based on the review of information currently available for the species conducted here, several main uncertainties associated with understanding of stock structure can be identified:

1. *Spawning dynamics.* An important part of understanding the natal origins of individuals is a detailed knowledge of the location and timing of spawning, and ultimately the number and geographical

extent of spawning units. For each of the four tunas reviewed here, spawning is considered to take place in waters $> 24^{\circ}\text{C}$ which, if water temperature alone is used to predict spawning location, would result in spawning occurring across large regions of the Pacific Ocean where and whenever temperatures are suitable. Several authors posit that actual spawning areas, however, may be more spatially and temporally variable than predicted by water temperature alone (Reglero et al., 2014; Muhling et al., 2017). A number of temporally-consistent spawning 'hot spots' have been observed for yellowfin and bigeye tunas (e.g., McPherson, 1988, 1991; Gunn et al., 2002; Servidad-Bacordo et al., 2012), supporting this theory. A comprehensive assessment of spawning activity, including both spatial patterns and associated timing of spawning (particularly identifying temporal overlaps or offsets between locations), examined in conjunction with known information on mesoscale oceanographic features such as eddies, currents and upwellings, would provide a key first-step in better understanding the spatio-temporal structuring of the spawning dynamics of each species. Examination of a range of data sources, including larval distributions from scientific surveys, the stomach contents of predators of larval tuna, large catches by set in longline fisheries (that target older and larger fish, and thus may indicate spawning activity), records of visibly spawning (i.e., running ripe) fish from fisheries observers, histological examination of previously collected gonad material and multi-year movement data from reproductively mature individuals, should help further resolve spatial and temporal dynamics in spawning of the four tunas.

2. *The degree of spawning area fidelity and localised residency.* For each of the four tunas covered here, it is currently unknown whether individuals i) spawn in different areas over the course of their life where and whenever conditions are suitable, or ii) spawn in the same general area throughout their life. If the latter, it is unknown whether they remain in close proximity to specific spawning areas or disperse widely after spawning and then return to the same area to spawn and, if they do, whether these movements represent fish returning to their natal spawning areas (i.e., natal homing). Because most tuna tagging studies in the Pacific Ocean have focused on juveniles using conventional tags, understanding of adult movement and the degree of spawning area fidelity is limited. Although some efforts have been made to examine movement of adults via electronic tagging approaches (Schaefer et al., 2007; Evans et al., 2011; Schaefer et al., 2011), existing data are largely inadequate for assessing potential spawning area fidelity. Studies assessing a combination of genetic and environmentally/physiologically-mediated attributes (e.g., otolith chemistry) of fish in spawning condition between different spatial strata may provide a suitable starting point for determining the degree of spawning area fidelity, and overall structure of stocks, of the four tunas. Modern genetic approaches, such as the use of NGS approaches and the identification of SNPs, have demonstrated a promising avenue for future research in this area (Casey et al., 2016; Pecoraro et al., 2017; Rodríguez-Ezpeleta et al., 2019). This approach offers numerous advantages over mtDNA and microsatellite-based approaches in stock structure studies, including the potential for higher genotyping efficiency, greater data quality and reliability, genome-wide coverage and analytical simplicity (Morin et al., 2004; Corander et al., 2013). The advent of NGS approaches provides a better representation of the genome and the identification of loci that are potentially under selection (so-called outlier loci), increasing the power to discriminate between weakly differentiated populations by disentangling between neutral evolutionary processes (i.e., genetic drift) and those influenced by selection (e.g., local adaptation) (Grewe et al., 2015; Pecoraro et al., 2017; Anderson et al., 2019c). However, a carefully designed sampling strategy that provides for representative sampling and includes spatial and temporal replication is needed to avoid introducing bias into such studies, such as those associated

with the sampling of multiple spawning units at the same location and time. Increased deployment of electronic tags, particularly on adults in running ripe condition, may further elucidate the degree of spawning area fidelity within the four species, and help resolve patterns in spawning activity observed through other methods.

3. *The provenance of individuals in, and proportional contributions of self-replenishing populations to, fishery catches within the Pacific Ocean.* A key challenge for management of tuna fisheries in the Pacific is understanding the proportion each potential self-replenishing population, or stock, contributes to harvested assemblages. This is particularly important given that i) fishing mortality is unevenly distributed across the region, ii) there is the potential for fisheries to exploit individuals from several stocks, if present, more-or-less simultaneously, iii) different stocks, if present, may have differing levels of productivity, and iv) there is potential for local depletion, particularly for less productive stocks, if they are structured in such a way that they are subject to higher fishing mortality. Although some studies have explored provenance and mixing across small spatial scales (Gunn et al., 2002; Wells et al., 2012; Rooker et al., 2016), expanding this work to scales relevant for regional fisheries management has yet to be undertaken. To do this effectively, co-ordinated and intensive systematic sampling efforts will be required, including extensive spatial and temporal components. Mixed stock analyses, incorporating complementary approaches such as examination of SNPs, otolith chemistry, and parasite assemblages, provide one potential approach for testing specific hypotheses about natal origins, movement and mixing of post-larval assemblages and the proportional contributions of source populations to fisheries. Mixed stock analyses have been used to clarify stock or population structure in a range of highly mobile species where adult assemblages may represent a mixture of individuals from different origins, including Pacific bluefin tuna (Shiao et al., 2010) and, at restricted spatial and temporal scales, for yellowfin, bigeye and South Pacific albacore tunas (Wells et al., 2012; Macdonald et al., 2013; Rooker et al., 2016).
4. *Linkages with adjacent 'stocks'.* Historically, the South Pacific albacore tuna population was considered to be distinct from individuals in the North Pacific Ocean. However, recent evidence suggests that some gene flow may occur between these regions (Montes et al., 2012; Albaina et al., 2013; Laconcha et al., 2015). Similarly, linkages between the South Pacific albacore tuna stock assessed in the WCPFC and individuals to the east are unknown. For bigeye tuna, differences between some components of adjacent stocks, such as individuals in the eastern Indian Ocean and those in Indonesian waters, in the far WPO, appear to be less clear-cut than previously thought (Proctor et al., 2019). Inclusion of samples from outlier areas in any sampling program is required to adequately assess stock relationships beyond currently accepted boundaries for the stocks. Inclusion of samples from adjacent stocks may further facilitate the development of an origin traceability tool that may enable the development of population-specific quotas (Rodríguez-Ezpeleta et al., 2019) and help curb illegal, unregulated and unreported (IUU) fishing.
5. *Effects of climate change on stock structure and proportional contributions of self-replenishing populations to fisheries.* Recent projections using SEAPODYM suggest that under climate change, shifts in the distribution of skipjack and yellowfin tunas at the basin scale are likely to occur (Senina et al., 2016, 2018). Current modelling approaches, however, are based on assumptions of single rather than multiple stocks for each species of tuna. Understanding how the introduction of spatial structure into the parameterisation of models used to investigate the responses of tuna populations to climate change might influence overall projections for population distributions is contingent on obtaining a better understanding of the uncertainties described above.
6. *Implications of improved knowledge of tuna stock structure for stock*

assessment and climate change model assumptions and fisheries management. The spatial scale and structure of Pacific tuna stock assessments have been based on tRFMO management boundaries, the nature of the fishing fleets exploiting each species, and the parameterisation of inputs required to achieve a robust model. Prior to undertaking sampling programs and analyses to determine the stock structure of tuna species, it would be prudent to simulate the extent to which different hypothetical stock structures might affect current stock assessments approaches and the associated management measures. The WCPFC is currently in the process of developing management procedures for the main tuna species that will allow for pre-agreed decisions for management action to be tested for robustness to plausible hypotheses of environmentally-driven movement (WCPFC, 2014; Scott et al., 2019a, 2019b), and a similar approach could be used to test robustness to different stock structure scenarios. The process can also examine the value of new information in terms of its potential to improve decision making, thereby providing further support for undertaking research activities. Similarly, models such as SEAPODYM could be used to examine the responses of multiple putative stocks of skipjack and yellowfin tunas, for example, to compare the composite redistribution of tuna biomass from these stocks due to climate change with projected redistribution of biomass from modelling a single, panmictic stock.

4. Conclusions

Although current assessments of skipjack, yellowfin, bigeye and South Pacific albacore tunas within each of the WCPFC and IATTC Convention Areas typically assume that each species forms a single stock, several lines of evidence reviewed here identify the potential occurrence of multiple stocks of each species within the Pacific Ocean basin at varying spatial scales. To better define the stock structures of Pacific tunas, and the underlying mechanisms by which spatial structuring occurs, uncertainty needs to be reduced in understanding of spawning dynamics (including any potential fidelity to particular spawning areas), origins and mixing of post-juvenile assemblages, and the proportional contributions of spawning units to mixed fisheries assemblages. More powerful and cost effective genetic and genomic tools, in particular NGS approaches and modern molecular markers such as SNPs, combined with complementary approaches based on otolith chemistry and parasites and well-designed electronic tagging experiments, provide a promising way forward for testing specific hypotheses regarding uncertainties around the presence of self-replenishing populations and their contributions to harvested assemblages. It is recommended that management strategy simulations and climate modelling, based on various hypothetical scenarios of stock structure, be thoroughly evaluated for each species to determine how an improved understanding of stock structure would influence the management of tuna stocks and implementation of adaptations to reduce the impacts of climate-driven redistribution of tuna species on island economies.

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